SHOUT
SHARE
IT

7.1.83

S.BM.
1020

A REAPPRAISAL OF *PROPHAETHON SHRUBSOLEI* ANDREWS (AVES)

C. J. O. HARRISON
AND
C. A. WALKER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 1
LONDON: 1976

A REAPPRAISAL OF *PROPHAETHON SHRUBSOLEI* ANDREWS (AVES)

BY

COLIN JAMES OLIVER HARRISON

AND

CYRIL ALEXANDER WALKER

Pp. 1–30 ; 3 *Plates* ; 7 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 1
LONDON : 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 27, *No.* 1, *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 4 *February,* 1976 *Price* £2.85

A REAPPRAISAL OF *PROPHAETHON SHRUBSOLEI* ANDREWS (AVES)

By C. J. O. HARRISON & C. A. WALKER

CONTENTS

		Page
	ABSTRACT	3
I.	INTRODUCTION	3
II.	DESCRIPTION	4
	a. Skull morphology	4
	b. Postcranial elements	11
	c. Measurements	16
III.	COMPARISONS WITH RECENT MATERIAL	18
IV.	DISCUSSION AND CONCLUSIONS	24
V.	SYSTEMATIC DESCRIPTION	27
VI.	ACKNOWLEDGEMENTS	29
VII.	REFERENCES	29
VIII.	INDEX	29

ABSTRACT

Prophaethon shrubsolei Andrews of the Lower Eocene, known from an imperfect skeleton, has been previously assigned to the Phaethontidae within the Pelecaniformes. After further preparation the specimen is redescribed. In comparison with Recent species of Pelecaniformes, Charadriiformes and Procellariiformes it was found to share some characters with all three, and could not with any certainty be assigned to any one of them. It is proposed, therefore, that *Prophaethon* should be considered as a representative of a new monotypic order, Prophaethontiformes, and it is suggested that it represents an early link between these Recent orders. This hypothesis is discussed and a diagnosis of the new order is given.

I. INTRODUCTION

IN 1899 C. W. Andrews described a fossil bird which W. H. Shrubsole had collected from the London Clay of the Isle of Sheppey, Kent, and had presented to the British Museum (Natural History). When found, the specimen consisted of a clay nodule in which one side of the skull and limb fragments were exposed. It was partially prepared at the Museum and when described and figured it showed the entire dorsal, posterior and right lateral views of the skull with the lower mandible in place. The orbit was also partly cleared of matrix back to the quadrate and down to the quadratojugal bar. The left side of the pelvis, which was somewhat obscured by the overlying skull, was also prepared, and a femur and the anterior portion of a broken tibiotarsus were laterally exposed.

From the general appearance of the skull Andrews concluded that it belonged to a pelecaniform bird. In the subsequent discussion of its affinities only pelecaniform families were referred to, and one may conclude that once he had decided on its possible ordinal status he did not compare it with material other than that within this taxon.

He compared the specimen systematically with examples of the various pelecaniform families and concluded that it most nearly resembled the genus *Phaethon* which constitutes the family Phaethontidae. In spite of some differences he thought that it was ancestral to *Phaethon* and named it *Prophaethon shrubsolei*, regarding the general similarities of the skull and deep fronto-nasal hinge with a prominent frontal ridge as evidence of affinity.

He noted that the nostrils of *Prophaethon*, unlike the holorhinal ones of *Phaethon*, approximated to the schizorhinal condition, but quoted Pycraft (1898) to the effect that on the skull of the young of *Phaethon* the nostrils show a nearly schizorhinal condition. He also noted that the pelvis was narrow and more closely resembled that of *Sula* and *Phalacrocorax*. He regarded the nostril condition as ancestral and concluded that the narrow pelvis indicated that, unlike the Recent *Phaethon*, *Prophaethon* was probably a good swimmer and diver, and that the extent to which *Phaethon* had diverged from this condition was a result of post-Eocene evolution.

During work towards a comprehensive review of the British Lower Eocene birds, still in progress, we decided that the specimen was suitable for further preparation by modern techniques. This was undertaken by Mr F. M. P. Howie of the Palaeontological Laboratory of the Museum. X-ray photographs were used to trace the position and extent of the bones present, and the specimen was then carefully prepared. As a result of this work most of the elements have now been separated and cleaned. The skull can be examined in all aspects including the palate (the lack of access to which Andrews regretted). The lower jaw is now separate and complete. A previously unsuspected portion of sternum has been revealed, and the hidden part of the proximal end of the tibiotarsus is now free. The pelvis has been extensively cleared, but still has attached to it the proximal half of the femur, and also portions of the ribs. An almost complete coracoid and the blade of a scapula are also present, and there are fragments of vertebrae and broken portions of limb-bones partly embedded in more resistant matrix.

In the following sections the various parts have been described. The terminology follows that of Jollie (1957) for the skull, and that of Howard (1929) for the post-cranial skeleton. From the characters now available the species does not appear to be closely allied to *Phaethon* and some characters are apparently shared with non-pelecaniform taxa.

II. DESCRIPTION

a. *Skull morphology*

CRANIAL AND ORBITAL STRUCTURES. Viewed dorsally (Fig. 1; Pl. 1, fig. A) and laterally (Fig. 2; Pl. 1, figs C & D) the skull as a whole shows a fairly even taper from its widest part in the temporal region to its narrow termination at the tip of the rostrum. The frontal rises a little from the dorsal edge of the parietals, with a slight inflation on either side in the area above the brain. From near the posterior edge of the orbits the frontal maintains a fairly even width anteriorly, with a shallow median hollow in the interorbital region, and then expands gradually at the anterior

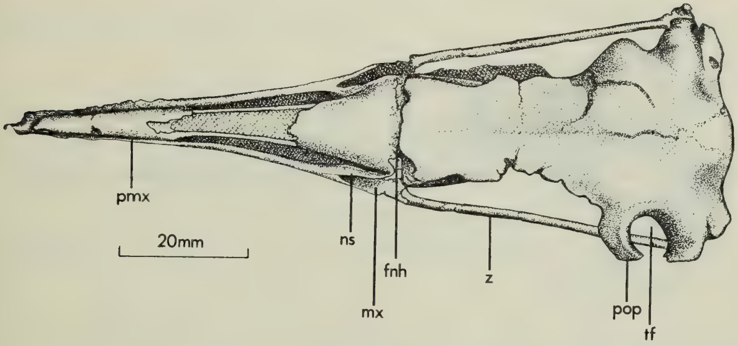


FIG. 1. Dorsal view of skull, × 1. Abbreviations : boc, basioccipital condyle ; bps, basiparasphenoid ; dps, gland depression, ? salt ; exn, external nares ; fm, foramen magnum ; fnh, fronto-nasal hinge ; ios, interorbital septum ; mx, maxilla ; ns, nasal strut ; pes, prefrontal attachment area ; pl, palatine ; pmx, premaxilla ; pop, postorbital process ; q, quadrate ; rps, rostroparasphenoid ; tf, temporal fossa ; z, zygoma.

end before terminating abruptly in a transverse, rounded and prominent brow ridge just above the fronto-nasal hinge. From the more complete left side of the frontal end of the specimen it would appear to be thick anteriorly, but above the orbits the frontal becomes very thin and its outer edge may have been irregular.

The posterior dorsal edge of the orbit curves outwards and terminates in a prominent, posteriorly curved postorbital process, which projects at a level only a little below the dorsal surface of the frontal. Posterior to this process is a deep temporal fossa. Viewed from above (Fig. 1 ; Pl. 1, fig. A), the fossa is rounded and partly enclosed by the postorbital process. In spite of the depth of the fossa the internal margin does not extend very far onto the dorsal surface of the cranium and there is only a relatively small and poorly-defined depression around its inner edge, while

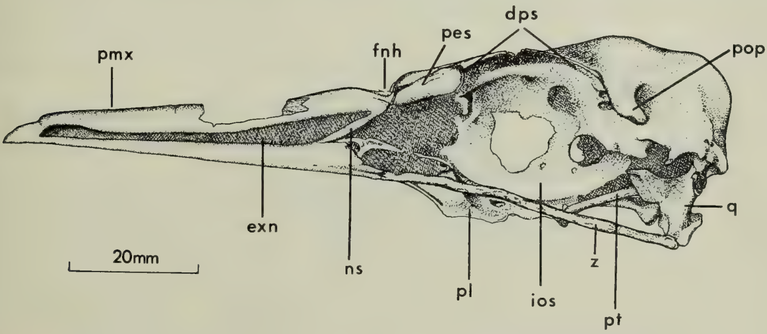


FIG. 2. Left lateral view of skull, × 1. Abbreviations as in Fig. 1.

posteriorly the main fossa slopes back to the line of the fronto-parietal junction. The fronto-parietal edge is superficially eroded and the original temporal fossa may have been more clearly defined.

Posterior to the fossa the squamosal and parietal form an arch over the auditory meatus with a slight peak marking the posterior edge of the fossa ; the quadrate articulates immediately below it. On the left side the outer edges of the bones are damaged, while on the right side both the postorbital process and the region above the quadrate are broken.

The cranium is rather small and projects forward medially with the result that, within the orbit, the posterior part of the frontal which forms the anterior ventral wall of the cranial cavity slants away postero-laterally, and also at an angle of *c.* 45° postero-ventrally.

In the upper region of the orbit the frontal is pierced, on either side of the interorbital septum, by a large oval fenestra opening into the cranial cavity. At the lower posterior edge of the frontal (or possibly in the orbitosphenoid) there is a large optic foramen, piercing the interorbital septum and extending laterally on either side of it. The septum itself is fragmentary and shows an extensive irregular central fenestra and various small subsidiary foramina. There are grooves, presumably to accommodate nerves, along the dorsal and ventral edges of the septum. The interorbital region of the frontal is thick, the roof of the orbit sloping from the orbit edge towards the septum.

At its anterior dorsal end the interorbital septum is pierced by a small, vertical fenestra which extends up into a hollow in the ventral surface of the frontal at this point. Just posterior to this fenestra the septum edge forms a thickened ridge descending from the orbit roof and curving forward below the fenestra, becoming concealed by the matrix which encloses the inner nasal region. The interorbital fenestra and hollow may have accommodated some structure with an olfactory function. This area is more complete on the left side of the specimen.

On this side the roof of the orbit shows a peculiar feature. Within the orbit, along its dorsal edge, there is an elongated oval depression, extending slightly inwards and terminating internally at an abrupt ridge where the frontal resumes its normal thickness. It is not clear to what extent the edge of the orbit may have been damaged, but there has been a reduction in thickness of the orbit roof, towards its edge, to accommodate a structure which was elongated, broader towards its middle, and dorso-ventrally flattened to an even thickness.

At the anterior end of the orbit the frontal is thick and abruptly flattened on the lateral surface. In some of the Recent Pelecaniformes this condition is associated with the presence of a closely attached but unfused prefrontal, which may fall away to reveal a similar surface of attachment. It therefore seems likely that a projecting prefrontal was originally present in *Prophaethon*, but has been lost. On the left side, within the orbit, there is an incomplete and laterally projecting flange of bone at the middle of the anterior edge of the interorbital septum. This might be the remains of the lateral ethmoid plate associated with it. In either case there is evidence for the existence of some structure at the anterior end of the orbital cavity, of a type normally associated with a prefrontal.

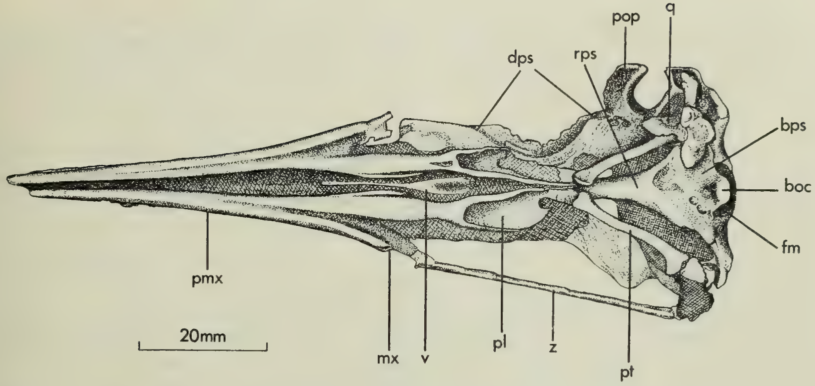


FIG. 3. Ventral view of skull with left zygoma removed, × 1. Abbreviations as in Fig. 1.

The jugal and quadratojugal form a narrow even strut of bone arising a little dorsal to the posterior tip of the maxillary and extending in a straight line back to the quadrate, continuing the line of the tomium of the upper mandible. The bar has been fragmented but appears to be laterally flattened along its entire length and shows no torsion.

Ventrally (Fig. 3; Pl. 1, fig. B), the basiparasphenoid is a small and triangular plate, tapering anteriorly to a smooth rostroparasphenoid and at the external posterior corners curving ventrally to form a pair of blunt projections only a little anterior to the occipital condyle. The area is damaged and pitted in places and it is not possible to be certain of the structure of the anterior part of the basiparasphenoid plate.

The posterior surface (Fig. 4; Pl. 1, fig. E) of the cranium is rather flattened, but a little inflated in the region of the supraoccipital. The foramen magnum is large and rounded and tilted slightly downwards. The parietals form a broad arch over the foramen. They are slightly hollowed dorsally towards the inner end, and the

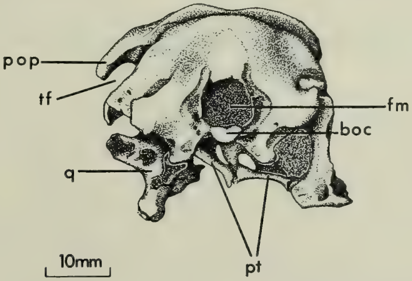


FIG. 4. Posterior view of skull, × 1. Abbreviations as in Fig. 1.

outer ventral edges are prominent and rounded posteriorly. The surfaces of the exoccipitals are concave. They have a slightly anterior ventral slant and begin to taper ventrally before expanding again at the line of fusion with the posterior edge of the basiparasphenoid plate.

QUADRATE. In *Prophaethon* the right quadrate is in the normal position with the shaft vertical, but it has been damaged along its external side. The left quadrate is also in position, but the posterior end of the pterygoid has become displaced upwards, allowing the quadrate to tilt inwards at its lower end ; it is held in this position by matrix on the internal side. The tilt has displaced the dorsal articulating surface and allows a better view of this end.

The shaft is postero-anteriorly flattened, the narrow waist at the level of the orbital process being about three times as broad as it is thick, and widening towards the dorsal and ventral ends. The dorsal head is laterally broad, the external flange of the otic process projecting laterally as far as does the quadratojugal socket on the ventral head. The otic process slants laterally from the waist to form a rather flattened process, with a shallow ridge from the base of the orbital process crossing the anterior surface, but with some of the posterior surface and tip broken away. The internal facet of the dorsal head appears to terminate as a rounded structure projecting internally only a little further than the inner edge of the shaft.

The orbital process is blade-like, with an almost horizontal upper edge and a slightly rounded tip. From this tip it curves down towards the lower part of the shaft. It appears to project anteriorly at an angle to the quadrate shaft of about 70°.

The ventral head of the quadrate is elongated laterally. The quadratojugal socket projects laterally and curves forwards so that the entrance of the socket is more anterior than the lateral alignment. The posterior side of the head curves back from the articulation socket to form a projecting posterior flange ; from the posterior side of the broken right quadrate of the specimen it would appear that there is a fairly deep but small groove on the lower end of the mid-shaft, cutting into the flange. The ventral surface of the quadrate then curves anteriorly again, but on the specimen the mandibular articulation surface of this region is damaged.

PALATE (Fig. 3 ; Pl. 1, fig. B). The skull presents an example of a typical schizognathous palate. The maxillae are broadest posteriorly at the point where they fuse with the palatines, and posteriorly they then taper rapidly on the external side to the articulation with the jugal. Anteriorly, they taper a little and extend for most of the length of the rostrum with a narrowing gap between them, fusion presumably occurring in the premaxillary region at the tip of the rostrum (now lost). They are slightly hollowed ventrally and the external edge projects ventrally to form the tomium of the upper mandible. The palatines arise near the posterior ends of the maxillae and extend back as shafts of similar width to the maxillae, but tapering a little, and then expanding in the region below the orbits, to form elongated, ventrally-hollowed blades, their posterior ends articulating with the pterygoids. The posterior external sides of both blades are a little broken but together they show the line of the external and posterior edge.

The palato-maxillae arise on the internal edge of the palatines near the region where the latter diverge from the maxillae. They extend posteriorly as narrow blades lying alongside the internal edge of the palatines, but from the side view of the skull it can be seen that they are laterally flattened blades with the upper edges curving dorsally and externally on either side of the vomer. Laterally, in the angle between the nasal bars and the posterior end of the maxilla, this upper edge of the palato-maxilla can be seen on the right side of the specimen as a projecting flange level with the junction of the nasal and maxilla ; on the left side it is broken, revealing the narrow extensions where it joins the internal ventral and internal dorsal ends of the maxilla.

Dorsally, the internal edge of the palatines extends upwards on either side of the anterior ventral edge of the interorbital septum, its posterior edge curving inwards and downwards to meet the posterior dorsal surface of the vomer. This structure is fairly complete but a little broken along its upper edge on the left side, and more extensively broken, but still showing curvature, on the right side.

The pterygoids are slender shafts. In ventral and lateral view the anterior end which articulates with the posterior tip of the palatine can be seen to be expanded, the sides diverging fairly evenly towards the tip on the ventral surface and with a prominent rounded dorso-external end visible laterally. The main shaft shows some lateral flattening and where it articulates with the right quadrate it shows dorso-external torsion and a rounded, blade-like expansion at the posterior dorsal end. This appears to increase the extent of the articulation with the internal side of the ventral end of the quadrate.

ROSTRUM. Where it joins the skull the rostrum is almost square in transverse section, but slightly narrower dorsally ; anteriorly it tapers very gradually to a point. The frontal region of the skull terminates in a bold ridge, bordered anteriorly by the deep, transverse fronto-nasal hinge. From the base of this ridge a rather flat nasal surface of the basal rostrum projects anteriorly, merging into the premaxilla, and tapering and becoming more rounded dorsally towards the anterior end. On either side it is separated from the more ventrally situated maxillae by an elongated aperture which also tapers and which extends to near the distal tip of the rostrum. Two slender bars of the nasal slope posteriorly upwards from the posterior part of the maxillae just where these widen, and appear to fuse laterally with the edges of the broad posterior rostral surface just anterior to the fronto-nasal groove.

MANDIBLE (Fig. 6f ; Pl. 2, figs A–C). The mandibular rami are slender, elongated and with only a gradual taper towards the tip. They have been twisted and show a dorsal torsion to the right. The distal end is damaged but the more proximal and articular regions are complete. The dentary portion of each ramus is moderately rounded externally, more marked towards the ventral edge. The internal side of the dorsal edge slants ventro-laterally, and ventral to this a deep groove occupies the centre of the internal surface, extending along the distal two-fifths of the mandible. Proximal to this groove the internal surface is rounded with a more prominent central ridge, continuing the internal tomium edge and gradually descending

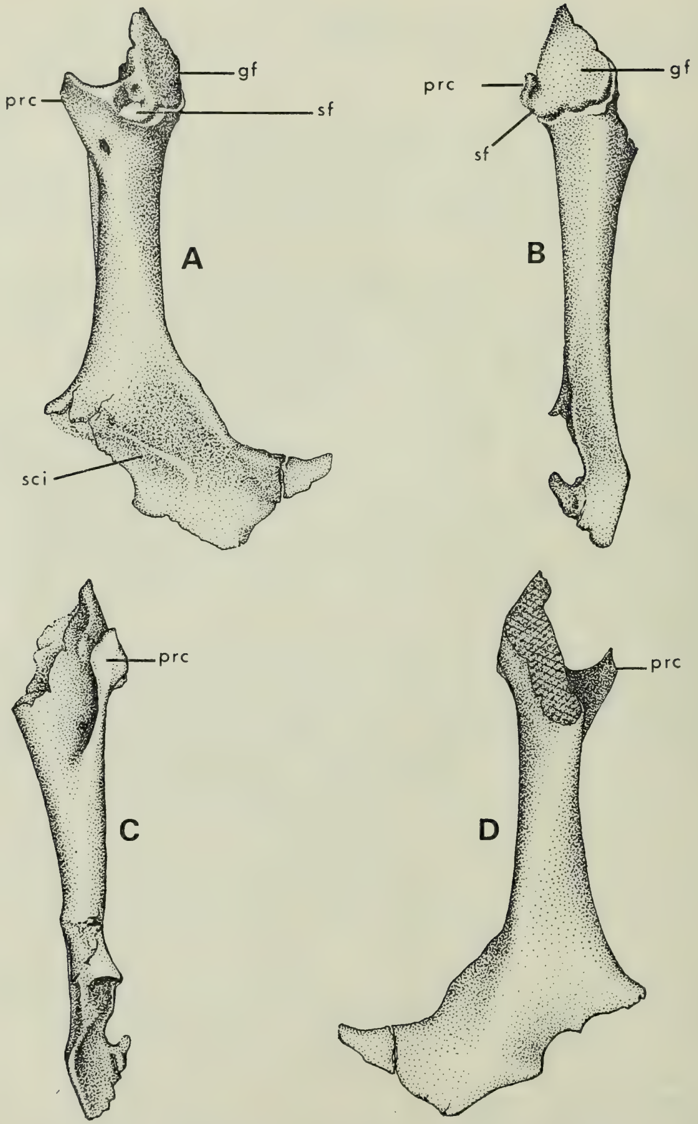

gf
prc
sf
A
sci
prc
gf
sf
B
prc
C
prc
D

Fig. 5. Views of right coracoid, × 2. A, dorsal; B, external; C, internal; D, ventral. Abbreviations: gf, glenoid facet; prc, procoracoid; sci, sternocoracoidal impression; sf, sternal facet.

ventrally and becoming shallower, to disappear near the ventro-posteriorly slanting mandibular suture. On the internal side (Fig. 6f), the upper edge of the splenial extends about three-quarters of the way along the ventral anterior edge of the suture and then extends anteriorly and ventrally as a thin line.

The mandibular suture appears as a deep groove internally, and much of the lower half is occupied by a narrow, elongated fossa, at the anterior end of which a narrow slit forms the internal opening of a poorly-defined anterior mandibular fenestra. Externally (Pl. 2, fig. C) the upper part of the suture is fused, but there is a narrow, elongated fossa, the dentary edge ventral to it projecting slightly so that the fossa is internal to it rather than dorsal. The upper edge of the fossa forms an external opening for the fenestral slit. Posterior to this external fossa the suture extends back ventro-posteriorly between the dentary and the anterior ventral parts of the supra-angular and angular. From the anterior end of the fossa a shallow and broad but well-defined groove extends almost horizontally along the external face of the dentary and terminates at a level a little posterior to that of the posterior end of the groove on the internal face of the mandible.

On the broad, internal face of the posterior part of the mandible, towards the dorsal edge, there is a large, oval, posterior mandibular fossa between the pre-articular and supra-angular. Since this is filled with matrix the internal structure is not visible, but it does not penetrate to the external surface.

Posterior to this fossa the mandible becomes less deep, but broadens rapidly just before the surface of the articulation with the quadrate. Dorsally, the surface widens rapidly into a triangular, smooth surface with a small articular prominence at the external corner. On the posterior side of the surface is a deep hollow which articulates with the ventral head of the quadrate. It has a complete dorsal rim on the external side, but elsewhere slopes to a median groove which occupies the centre of an extension of the hollow opening into the internal side. Posterior to the hollow the dorsal surface terminates as a narrow edge, broadening at the internal end into a small triangular surface with a raised and rounded internal tip, and on the inner side of this, broadening the posterior edge of the hollow, there is a small rounded foramen.

The posterior surface of the mandible is flattened and forms a modified inverted triangle. It has a distinct and narrow dorso-internal protrusion, while the lowest part is more broadly rounded and projects as a narrow, curved lip beyond the main ventral shaft. The surface is hollowed at the centre. The true position of this surface is difficult to determine because of the torsion of the specimen, but it appears to show some internal deflection and a marked posterior-dorsal tilt, the ventral lip projecting beyond the rest of the structure.

b. *Postcranial elements*

STERNUM (Fig. 6a–c). The sternum was previously concealed within the matrix and its presence was not suspected until the present preparation had begun. It is still partially embedded in matrix and lacks its posterior end and the lateral posterior parts of the sternal plate. The carina, which lacks the posterior end, is exposed on its right side and along the anterior and ventral edges. In addition the

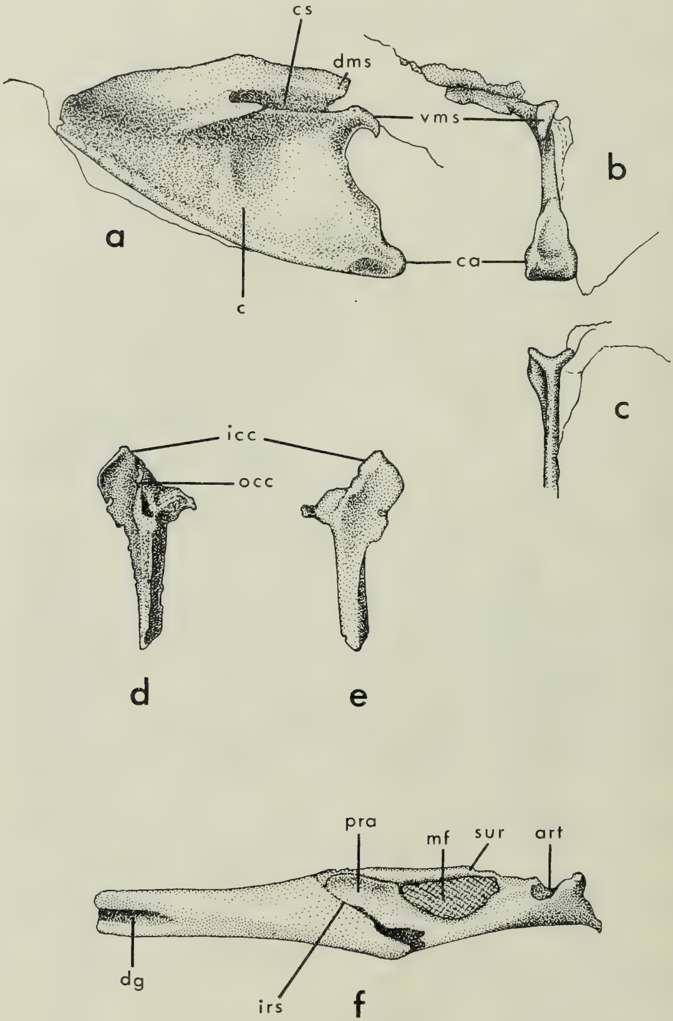


Fig. 6. Views of partly embedded sternum, × 1; a. right lateral, b. anterior, c. ventral. Views of imperfect left tibiotarsus, × 1; d. oblique anterior, e. oblique internal. f. View of the internal side of right mandible, × 1. Abbreviations: art, articular; c, carina; ca, carinal apex; cs, coracoidal sulcus; dg, dental groove; dms, dorsal manubrial spine; irs, inter-ramal suture; mf, mandibular foramen; occ, outer cnemial crest; pra, prearticular; sur, surangular; vms, ventral manubrial spine.

ventral manubrial spine and right half of the manubrium and coracoid sulcus are also present. The right half of the sternal plate is shattered posterior to the thickened region of the sulcus and lacks the external and posterior parts.

The sternal plate shows slight ventral curvature. The carina is large, projecting ventrally and anteriorly, with a slight curvature of the ventral margin. It becomes thicker anteriorly, and at the carinal apex bifurcates to accommodate the ventral end of the anterior articulating surface. The anterior carinal margin is stout, but tapers at the dorsal end where it curves up to the underside of the ventral manubrial spine. The latter is a small sharp projection, an inverted triangle in transverse section with the wider dorsal surface rising slightly anteriorly and then curving forwards and downwards, tapering away to a point a little below the level of the ventral edge of the spine.

The anterior carinal margin curves forwards ventrally, its apex anterior to the tip of the spine. The upper part, about three-fifths of the whole, curves forwards and becomes thicker ventrally, and forms a blunt projection at a similar anterior level to the tip of the manubrial spine. Below this, the remaining two-fifths form a flattened, elongated anterior facet, hollowed centrally and curving forward ventrally. It appears analogous to similar surfaces on the sterna of some pelecaniform species, which articulate with the furcula in the region of the ventral symphysis. Viewed laterally (Fig. 6a), this surface on *Prophaethon* is hollowed to such an extent that it shows some posterior curvature. Viewed anteriorly (Fig. 6b) it is dorsoventrally elongated and wedge-shaped, widening ventrally and with the ventral portion curving anteriorly. At the ventral end the hollow becomes shallower, forming a poorly-defined lip below the deepest part of the cavity.

The dorsal lip of the coracoid sulcus appears thickened but is superficially damaged. The ventral lip arises at the lateral dorsal edge of the base of the ventral manubrial spine and slants posteriorly across the sternal plate. There is a broad ventral surface between the anterior edges of the dorsal and ventral lips. The ventral labial prominence occurs about two-thirds of the way along the sulcus as a bluntly rounded, thin flange overlapping the sulcus which up to this point appears to be ventrally exposed. A low ridge across the sternal plate from the posterior part of the carina terminates at the sulcus after crossing the ventral surface of the ventral labial prominence.

The sulcus terminates a little lateral to the prominence, the ventrally projecting ridge of the dorsal lip curving posteriorly towards the end of the sulcus to leave a thinner, laterally-projecting, area of the sterno-coracoid impression.

Coracoid (Fig. 5; Pl. 2, figs D–G). The right coracoid is preserved, but anteriorly it is broken off just above the glenoid facet, the broken surface extending along part of the ventral edge. The sterno-coracoid process and internal distal angle are also damaged.

The shaft is smooth and rounded, but towards the distal (sternal) end it is dorsoventrally flattened. The sterno-coracoid surface is large and slightly curved ventrally, and since the dorsal lip of the coracoid sulcus is markedly anterior to the ventral lip, as already described in discussing the sternum, the ridge marking the articulating surface for the latter appears across the middle of the dorsal surface of the sterno-coracoid area. It becomes lower and disappears before reaching the flattened and rather rectangular sterno-coracoid process. The internal distal angle of the coracoid is broken off at the line of the articulation ridge.

The shaft becomes thicker and more rounded, and laterally narrower, as it approaches the procoracoid. From the faint scar of attachment of the coraco-brachialis a poorly-defined ridge crosses the shaft to the distal end of the procoracoid. The latter projects laterally and curves anteriorly and ventrally to a point (broken short in the specimen). On the internal side there is a curved hollow between the procoracoid and shaft, with a small longitudinal ridge on either side of it. The internal opening of the coracoid fenestra is a small hole near the distal end of this hollow, and the external opening is a similar hole on the dorsal surface of the procoracoid, towards its edge.

The scapular facet is shallow and dorsal, and from it a thickened ridge borders the proximal edge of the procoracoid. The glenoid facet is dorsoventrally aligned. Ventrally, there is a low ridge from the ventro-external edge of the shaft, which crosses the sterno-coracoid process and terminates near its distal external extremity.

Scapula. The single left scapula lacks the proximal articulating end. It is a slender rod with a slight ventral curvature, dorso-ventrally flattened. It is a little thicker and more rounded at its base and towards its tip becomes more flattened and broader, then tapers to a point.

Pelvis (Pl. 3, figs A–C). Most of the pelvis is present. At the anterior end of it a row of laterally crushed vertebrae form the relic of the thoracic part of the vertebral column. Dorsally the pelvis has been cleared of matrix but some of the more ventral detail of the left side is still obscured by matrix containing broken ribs. On the right side it is completely exposed. The anterior lateral edge of the ilium is broken on the right, but appears complete on the left side. Posteriorly, on the right, the ischium and pubis are broken off at about the posterior end of the ilio-ischiatic fenestra, and the ilium posterior to the fenestra is also missing, the dorsal end terminating at the incomplete caudal end of the synsacrum. On the left side, part of the iliac portion of the synsacrum is visible and the ventral struts of the roof of the renal depression can also be seen on the left.

At the anterior end of the pelvis the median-dorsal ridge is thick and prominent, appearing to fuse with the end of a row of elongated and flattened neural spines. The ridge projects sharply, the iliac plates sloping down steeply on either side and curving outwards to form a lateral flange, broadest anteriorly and with a rounded tip. Posteriorly the dorsal ridge widens and the iliac plates become narrower and less hollowed laterally. The edges of the ridge diverge as two well-defined edges of the anterior iliac crest, curving outwards to a slight prominence above and internal to the acetabulum. From there, two blunt, broad ridges continue posteriorly as the posterior iliac crest, curving slightly towards each other in the region of the ilio-ischiatic fenestra, before diverging posteriorly. The shield area between them is narrow and slightly hollowed, with a median ridge beginning to appear towards the posterior end ; on the left side at the posterior end there is what may have been the first of a double row of narrow fenestrae from the renal depression. Below the posterior iliac crests the iliac surface slopes outwards as a narrow upper edge to the iliac-ischiatic fenestra. The fenestra is large and elongated, becoming wider posteriorly, with a relatively straight lower edge, a posteriorly-curved upper edge, and the two meeting anteriorly in a small rounded end just posterior to the lower edge of the antitrochanter. Anteriorly the surface bordering the upper edge of the fenestra flares out to a prominent lip over an antitrochanter, the articulating surface of which has an anterior/external aspect and also an anterior/ventral slant. Below this is a rounded acetabulum, the lower third of which does not penetrate completely to the ventral side, but forms a rounded hollow in the bone. There is a small lateral projection midway along the anterior external edge of the acetabulum.

Just ventral to the anterior edge of the acetabulum a small anteriorly-projecting pectinal process is present, posterior to which the pubis slopes away as a slender rod of bone. The anterior end of the ischio-pubic fenestra is narrow but rounded and terminates posterior to the ventral edge of the acetabulum. Dorsal to it the ischial bar is nearly twice the width of the pubis. Just posterior to the acetabulum the external surface of this ischial bar slopes ventro-internally, until it meets a small ridge which slopes back from the posterior edge of the antitrochanter, at which point torsion occurs and the external face of the ischium has a ventro-external slant, and shows a poorly-defined, posteriorly and ventrally slanting, ridge in its surface.

The fused synsacrum has its greatest depth at the anterior end and viewed laterally the dorsal line of the pelvis and the ventral surface of the synsacrum converge towards the posterior end, forming a thin elongated wedge that shows a slight ventral curvature at its posterior tip. The ventral surface of the synsacrum is widest at the region of the sacral vertebrae, where it shows a well-defined median groove, and tapers gradually towards the posterior end. Anteriorly it also begins to taper but becomes broader again at the anterior tip where it articulates with the first free vertebra. The latter appears to be the last dorsal vertebra. The anterior articulation surface of the synsacrum is posterior to the broad dorsal anterior edge of the ilium.

FEMUR. The right femur was exposed in the specimen as originally prepared ; it appears from the original figure (Andrews 1899) to have had a coating of matrix and to have been superficially damaged beneath this. The present preparation has exposed on the distal half, which is detached from the main block but still attached to the tibiotarsus, an internal distal surface almost to the condyle ; on the proximal half still *in situ* on the pelvis the external and posterior surfaces are visible.

The distal internal face shows a smooth, slightly rounded surface with a rounded and posteriorly projecting condyle, the internal condylar surface showing an internal deflection towards the distal end.

The trochanter shows an abrupt obturator ridge with a hollow beneath it on the posterior side. The anterior head of the trochanter is rounded, and the external edge appears to form a blunt, projecting ridge which extends for some way along the anterior external edge of the shaft.

Tibiotarsus (Fig. 6d–e ; Pl. 3, figs D–E). During preparation the proximal end of the left tibiotarsus was removed and cleaned. The external side of the shaft had originally broken away as far as the head, but the internal side is still intact.

The anterior and internal sides of the shaft are present and where they join there is an abrupt edge which becomes more prominent towards the proximal end and finally forms the anteriorly-projecting flange of the inner cnemial crest. The inner cnemial crest is a thin prominent flange arising along the internal edge, projecting anteriorly and at its outer edge curving a little externally. It extends proximally well beyond the articulating surfaces. It arises gradually from the shaft, is deepest at about the level of the proximal edge of the articulating surfaces, and then tapers to a blunt point proximally. The outer cnemial crest arises on the anterior surface near the external edge and nearer the proximal end than does the inner crest. It is thicker distally than the inner cnemial crest and projects at an angle between the anterior and external surfaces, curving slightly towards the external side. Its proximal end terminates at an angle a little proximal to the articulation surfaces. It appears to end abruptly as though broken short but this is also apparent on some entire examples of Recent species.

The internal articular surface is more distally placed than the inter-articular area and the ends of the crests. Its surface is damaged on the specimen, but it shows a posteriorly-projecting, curved lip. The inter-articular area slopes distally on the external side, curving distally to the broken external surface in a shallow hollow on the external side of the outer cnemial crest.

Ribs and other elements. The head of a rib and part of another are visible on the left side of the specimen anterior to the pelvis, together with broken shafts still embedded in matrix. The visible head is relatively stout ventral to the tubercle, and the portions of shaft are fairly broad. There is no obvious uncinate process, but a slender and flat strip of partially embedded bone parallel to the left posterior iliac crest might be referable to this. In general structure the ribs resemble those of the larger larids and sulids.

In addition to the material described above, there are also a number of fragments of bone and matrix removed during preparation. A close examination of these might make their identification possible, but they are not likely to provide additional useful information to the present study. Their existence is therefore noted, but no further study has been made.

c. *Measurements*

All dimensions are given in millimetres.

Skull

Overall length (premaxilla–supraoccipital)	112
Maximum width at posterior end (squamosals)	35·5
Maximum width at postorbital processes	38
Minimum width of interorbital bar	15
Width at anterior end of frontals	16·7

SKULL (continued)

Width at base of rostrum (dorsal)	15·8
Width at base of rostrum (ventral)	20
Mid-rostral width	10
Width at tip of rostrum as preserved	3·8
Length of culmen	61
Length of lateral nasal aperture	50·4
Maximum depth of lateral nasal aperture	3·4
Posterior depth of cranium to occipital condyle	19·5
Maximum cranial depth	24.5
Depth from anterior end of frontals to palatines	19·9
Width of temporal fossa at postorbital process	6·1
Minimum width of cranium at temporal fossae	26
Length of dorsal hollow in orbit (? nasal gland)	22
Width of dorsal hollow in orbit (estimated)	4
Length of palatines	42
Maximum proximal width of palatines	5·6
Length of pterygoid	1·8
Width of shaft of pterygoid	1·6
Width at quadrato-pterygoid articulation	4·3
Maximum width of posterior end of basiparasphenoid plate	17
Width of rostroparasphenoid	3·2
Length of zygoma	44·2
Depth of zygoma	2·6
Width of zygoma	1·3

QUADRATE

Quadratojugal socket to otic process	14·5
External–internal width of quadrato-articular surface	12
Anterior–posterior width of quadrato-articular surface	5·9
External–internal thickness of shaft below orbital process	4·8
Maximum depth of orbital process	6·2
Length of orbital process	7·8

LOWER MANDIBLE

Maximum length of left dentary to post-articular process (incomplete)	109·9
Maximum length of right dentary to post articular process (incomplete)	112·2
Depth of dentary at tip	4
Width of dentary at tip	1·9
Depth of dentary at proximal end of internal dentary groove	6·7
Width of dentary at proximal end of internal dentary groove	3·7
Maximum depth of dentary at intraramal suture	13·2
Maximum width of dentary at intraramal suture	2·3
Depth at anterior end of articular surface	6·5
Width at anterior end of articular surface	9·1
Depth at posterior end of articular surface	9·3
Width at posterior end of articular surface	11·2
Maximum length of posterior mandibular fossa	14·3
Maximum depth of posterior mandibular fossa	6·7

SCAPULA

Overall length (incomplete)	67·7
Maximum distal width	6·2
Proximal width	4·9
Thickness at proximal end	2·7

CORACOID

Overall length	43·2
Maximum distal width	19·9
Width of glenoid facet	6·1
Width of scapula facet	2·1
Width of sternal facet	5
Width of shaft at coracoidal fenestra	6·8
Internal–external length at sternal facet (left)	20·2
Proximodistal width of sternocoracoidal process (left)	8·5

Sternum

Maximum length to ventral manubrial spine	51·5
Length of carinal edge (incomplete)	59
Carinal apex to dorsal edge of ventral manubrial spine	26·5
Tip of ventral manubrial spine to anterior carinal margin	6·3
Length of furcular facet	10·9
Maximum width of furcular facet	6·8
Tip of ventral manubrial spine to ventral labial prominence	22·1
Width of coracoidal sulcus	5·7

Pelvis

Maximum medial length as preserved	67
Anterior border of ilium to anterior edge of acetabulum	35
Maximum width across antitrochanters	27·4
Anterior width from external edge of ilium to medial ridge	17
Length of ilio-ischiatic fenestra	23·3
Maximum depth of ilio-ischiatic fenestra	10
Minimum distance between antitrochanter and pectineal process	14
Ventral length of synsacrum	69·5
Anterior depth of pelvis from median dorsal ridge to synsacral thoracic vertebra	19·5
Width of articular facet of first synsacral thoracic vertebra	7·5

Femur

Proximodistal length	51
Anterior/posterior thickness at mid-shaft	4·8
Maximum proximal width at trochanteric ridge	9·4

Tibiotarsus

Length as preserved	31·3
Articular surface to tip of internal cnemial crest	6·1
Maximum width of internal cnemial crest	5·2
Width from internal edge to external edge of internal cnemial crest	15·5
Width to internal edge of internal cnemial crest	8·6
Width to external edge of outer cnemial crest	14

III. COMPARISONS WITH RECENT MATERIAL

In attempting to place *Prophaethon* within the framework of avian taxonomy, using the characters revealed by further preparation, it has been necessary to compare it with osteological material from various Recent taxa. Since the earlier claims of pelecaniform similarities were based on skull characters it seemed preferable for comparative purposes to begin at the other extremity.

Proximal end of Tibiotarsus. The obvious characters on this element are the prominent inner cnemial crest, which has its widest part just above the level of the articulation surfaces and tapers proximally, and the inner cnemial crest forming a blunt projection at a similar level. The proximal articular surface slopes posteriorly and has a projecting lip with a concave proximal surface at the posterior edge. The external edge of the proximal surface curves smoothly over onto the shaft in a broad zone where it borders the inner cnemial crest.

Stercorarius provides a very close match in all aspects, while other Charadriiformes also show resemblance to varying degrees. In the Procellariiformes *Diomedea* shows some similarities but lacks the projecting posterior lip, and has a larger and more proximally situated inner cnemial crest. There is no obvious resemblance to the Pelecaniformes, where *Phalacrocorax* retains only a short curved outer cnemial crest while *Sula* has small blunt projections. The features are almost entirely lacking in other pelecaniform genera.

FEMUR. This is long and narrow, the trochanteric crest present as a prominent narrow ridge rounded off at the proximal end with a curved muscle scar incised into the external surface. In the Charadriiformes the ridge is much more developed, both anteriorly and proximally. *Macronectes* in the Procellariiformes shows similarities to the specimen. *Sula* has a stout, curved femur, the proximal end of which shows some similarity to that of *Prophaethon*, but the trochanteric ridge is low and blunt and the head is more ventrally deflected.

PELVIS. The narrow, elongated pelvis is typical of that found today in birds which swim and dive to catch their prey. It bears no resemblance to that of *Phaethon*, which is broad and short.

The anterior shield of the ilium extends forward only as far as the proximal end of the second synsacral thoracic vertebra, and the third vertebra is unfused. This condition is typical of the Charadriiformes but not of the other orders examined here. *Sula* does, however, show a short anterior iliac shield.

The median dorsal ridge is slightly convex, but posteriorly it is depressed between well-defined posterior iliac crests. In this respect the specimen resembles *Phoebetria*, *Diomedea* and *Puffinus* among the Procellariiformes. The Alcidae show a similar profile. In the Pelecaniformes the posterior iliac crests are poorly developed and in the more aquatic forms such as *Sula* and *Phalacrocorax* the posterior median ridge is level with or dorsal to the lateral crests.

The Pelecaniformes also show more laterally projecting and anteriorly directed antitrochanteric surfaces than does *Prophaethon*, and in the latter the iliac surface immediately anterior to the acetabulum is concave and the pectineal process prominent. The specimen is more similar in these respects to both Procellariiformes and Charadriiformes, although among the last the Alcidae show the pectineal process greatly reduced or absent. From fine sutures apparent on the specimen the ilium would appear not to have been fused with the synsacrum, in this respect resembling Recent Alcidae and Procellariiformes rather than Pelecaniformes.

VERTEBRAE. The free thoracic vertebrae appear to lack hypopophyses. They have rounded concavities laterally, posterior to the prominent anterior costal facet. The diapophyses are short, dorsally broad and have a thin middle ridge ventrally with a deep concavity at the internal corner of the anterior side. There is a thin, tapering anterior process at the distal end of the diapophysis. These vertebrae resembles those of the larger *Larus* species in the Charadriiformes. Those of the Procellariiformes are more elaborate with larger concavities and various fenestrae, and with hypopophyses ; those of the Pelecaniformes show still fewer similarities to those of *Prophaethon*.

Sternum. Allowing for the incompleteness of the specimen the carina of the sternum is deep and long, extending further back than is the case on Recent Pelecaniformes. The ventral lip of the coracoid sulcus is posteriorly situated so that the sulcus is ventrally exposed, particularly at the middle region, but towards the outer end it undercuts a small but broad labial prominence.

In the Pelecaniformes the ventral lip of the sulcus extends almost as far anteriorly as does the dorsal lip, and the sulcus is a deep, anteriorly-directed groove. In *Prophaethon* the groove is more typical of that found in Charadriiformes and Procellariiformes. From the ventral labial prominence a distinct intermuscular line slants postero-internally towards the middle of the carina. A similar line is present in Charadriiformes, but in the Procellariiformes one line arises on the sulcus internal to the labial prominence and crosses the sternum more anteriorly, while another rises towards the external end and slants towards the posterior end of the carina. In Pelecaniformes there is a faint ridge from the labial prominence apparent in Phalacrocoracidae and Phaethontidae.

The hollow facet for furcular articulation at the anterior tip of the carina is a distinctive character in *Prophaethon.* Structures of this kind are found in some Recent species of Pelecaniformes and Procellariiformes. A small articulation surface is present on the larger Podicipitiformes. This furcular surface is more extensively developed in the Pelecaniformes where the Pelecanidae and Fregatidae have the furculum fused to the sternum while Phaethontidae, Sulidae and Phalacrocoracidae have the surface developed to varying degrees. Of the Procellariiformes the Pelecanoididae have a sternum with a large furcular articulation facet, its ventral edge curved anteriorly. The bifurcation of the carina tip, apparent in *Prophaethon,* is characteristic of many Procellariiformes but not of the Pelecaniformes. None of the Charadriiformes show furcular articulation facets on the sternum.

The shape of the manubrial spine in *Prophaethon* resembles that of *Phaethon,* but this structure differs so markedly in different families and genera that we do not regard it as taxonomically useful.

Coracoid. The shape of the sternal (distal) end of the coracoid is correlated with that of the coracoid sulcus. The coracoids of Pelecaniformes show sternal facets on both sides at the distal end, articulating with the deep sulcus. *Prophaethon* resembles charadriiform and pelecaniform birds in having a prominent facet across most of the dorsal surface ; a small one on the ventral surface towards the external end is correlated with the position of the ventral labial prominence of the sternum. From the fit of the specimen there is no reason to suppose that the missing internal distal angle of the coracoid of *Prophaethon* would have projected across the midline of the sternum, as in *Phaethon.*

A stout and dorsally curved internal distal angle to the coracoid is characteristic of most Procellariiformes, although less evident in the Pelecanoididae, and in the Laridae and Alcidae of the Charadriiformes. Although this part of the specimen of *Prophaethon* is damaged, the general shape of the surrounding bone and the sternal fragment of the other coracoid, which is also present, indicates an absence of such curvature. The specimen most closely resembles the flatter coracoids of *Ibidorhynchus* and *Haematopus* of the Charadriiformes in this respect; it also resembles them in the area of irregular surface on the dorsal side distal to the line of attachment of the coraco-brachialis muscle, the proportions of the shaft, the procoracoid, and the position of the coracoidal fenestra.

LOWER MANDIBLE. This, although relatively complete, does not give an indication of affinity with any particular taxon.

The slender ramus, increasing in depth posteriorly and tapering a little at the anterior end of the articular portion, has a general resemblance to those of Phalacrocoracidae and some Procellariidae. The tapering groove on the external surface anterior to the intraramal suture is similar to that of Procellariiformes and Charadriiformes, but a groove of this type is also present in *Phaethon*.

The arrangement of the component bones around the external fossa of the mandibular suture and the shape and position of the fossa itself are most closely paralleled by the structure in some smaller Laridae, the Burhinidae and to a lesser degree by some Procellariiformes. The concave, ventrally tapering and postero-dorsally oriented postarticular surface is very similar to that of Gaviiformes, but only resembles to a limited extent those of the other taxa examined here.

The articular facets are very similar to those of Laridae, Burhinidae and Procellariidae but do not closely resemble the more specialized structures of the Pelecaniformes.

Prophaethon has a large, rounded posterior mandibular fossa, bordered anteriorly by a large prearticular which extends anteriorly to border the mandibular suture and overlaps with, and possibly fuses with, the dentary towards the dorsal edge of the ramus. This large prearticular is also present in the Procellariiformes and Gaviiformes. The Charadriiformes have a large posterior fossa but the prearticular is small and only partially occupies the anterior space, the mandibular slit forming a distinct fenestra. *Phaethon* shows a similar condition but has the prearticular larger posteriorly, reducing the size of the posterior fossa. In the other pelecaniform families the posterior fossa is tiny and the prearticular has filled the remaining space.

SKULL. The palate is typically schizognathous and resembles those of Charadriiformes and Gaviiformes. Procellariiformes also have this type of palate, but the distal end is modified by bill shape. The palates of Pelecaniformes appear to be schizognathous in the very juvenile condition but desmognathous in the adults. Schizognathous palates are also present in Podicipitiformes, Gruiformes, Galliformes, Sphenisciformes and Columbiformes. The distinctive proximal bifurcation of the vomer, visible between the palatines in *Prophaethon*, is very similar to that of larger *Larus* species and of other Charadriiformes, but does not appear in Pelecaniformes and Procellariiformes.

The rostrum of *Prophaethon* is long, slender and tapering. An elongated nasal aperture runs for almost the whole length, rising posteriorly and tapering to a slit just proximal to the frontonasal hinge. In general shape the rostrum is similar to that of the Phalacrocoracidae, and if it were argued that the latter retained the open aperture of the juvenile there would be strong similarity. In other Recent birds the elongated nasal apertures are typical of Charadriiformes, Gaviiformes, Podicipitiformes and Gruiformes. Although the nares of Pelecaniformes are typically closed or minute, *Phaethon* shows an intermediate condition with a short but relatively large aperture about a third of the way along the rostrum and a tiny hole near the frontonasal hinge.

A transverse frontonasal hinge developed to differing degrees in different families is associated with the greatly reduced nostrils in Pelecaniformes. In *Prophaethon* the nasal apertures are schizorhinal in shape, but since the nasal struts join the rostrum anterior to the frontonasal hinge they are functionally holorhinal. A holorhinal type of nostril associated with a frontonasal hinge in this position also occurs in the Charadriiformes in the Burhinidae, Thinicoridae and *Pluvianus* of the Glareolidae, although charadriiform nostrils are usually collectively described as schizorhinal. A deep transverse frontonasal hinge comparable with that of the Phaethontidae also occurs in *Rhynchops* of the Charadriiformes, but in this instance the nostrils are schizorhinal. Procellariiformes have an unspecialized transverse frontonasal structure and holorhinal nostrils.

In the Pelecaniformes the heavy frontal brow associated with a deep frontonasal groove is present only in the Phaethontidae. In the Charadriiformes it is partially developed in *Rhynchops*, and more highly developed in the Chionidae. In the latter the nasal struts lie alongside the rostrum and also terminate just below this brow, apparently forming a hinge with the rostrum. This structure has some analogy with that of *Prophaethon* since a close inspection of the latter reveals that the nasal lies close alongside the dorsal rostral surface but may not fuse with it completely, and the transverse line of the frontal brow is not completely straight but shows paired lateral recesses in the fore-edge which might be comparable with those of Chionidae. Unfortunately the surfaces of the bone are slightly damaged at this point in the specimen of *Prophaethon*.

The frontal shows a flattened lateral surface suggesting the loss of an unfused prefrontal. Prefrontals are unfused in the Phaethontidae and Fregatidae of the Pelecaniformes, and in Burhinidae of the Charadriiformes; when they become detached they leave flat surfaces similar to those of *Prophaethon*.

The smooth dorsal surface of the skull of *Prophaethon* may have pelecaniform similarities, but only by virtue of the absence of the nasal glands, and were these not present in other taxa they might also be similar. The feature is therefore a generalized one, indicative of absence of specialization rather than affinity. In the deeply rounded temporal fossae posterior to the prominently curved postorbital process the specimen resembles the Fregatidae, *Uria* of the Alcidae and *Stercorarius* in the Laridae, rather than the Phaethontidae, but shows some similarity to the last in the rather limited development of the fossae dorsally and anteriorly.

In the area of quadrate articulation the ventral edge of the orbitosphenoid curves forwards, leaving a large cavity anterior and internal to the articulation surface and tending to divide the latter into two. This is also present to a similar degree in the Pelecaniformes, but much reduced in the Procellariiformes and Charadriiformes.

The posterior aspect of the skull of *Prophaethon* has parallels in all the major taxa here examined, and there are considerable differences in these at the family level. The supraoccipital of *Prophaethon* has a small foramen on either side towards the ventral edge, with associated grooves bordering the upper edge of the foramen magnum. Similar structures are apparent in the Procellariiformes, more modified in the Charadriiformes, and greatly modified or absent in the Pelecaniformes.

Within the orbit of *Prophaethon* the hollow apparently accommodating the nasal gland is in a unique position, being an elongated hollow bordering the dorsal edge of the orbit and on the ventral surface of it. In Pelecaniformes the nasal gland is usually towards the anterior dorsal end of the orbital hollow and in a more median position. In some *Phaethon* species a small elongated hollow extends posteriorly into the orbit from this anterior site, bordering the orbital septum but separated from it by the channel of the olfactory nerve. In the Sulidae it is an elongated hollow lying completely in the roof of the orbit, but still close to the septum. In Charadriiformes and Procellariiformes the nasal gland hollow either borders the dorsal edge of the orbit or lies internal to it, but on the dorsal surface of the frontal. The position of this structure in *Prophaethon* is therefore intermediate between that in the two Recent types.

The slender, unspecialized pterygoids of *Prophaethon*, with a small posterior lateral expansion of the orbital process of the quadrate, give little useful evidence of affinity. The Phaethontidae show an even less modified structure, but the pterygoids of other pelecaniform families and of the other taxa discussed here are stouter, with some development of lateral flanges on the shaft, and in several diverse taxa show the expanded posterior end.

The quadrate of *Prophaethon* also shows little evidence of affinities, and the deep groove at the ventral end of the posterior surface of the shaft appears to be a peculiarity of the species.

Tables 1 and 2 give a simplified summary of apparent similarities. Tables such as this may oversimplify, exaggerating both similarities and differences, but they indicate the problem involved in assigning *Prophaethon* to a known taxon.

TABLE 1

Comparison of postcranial elements of *Prophaethon* with extant orders of birds

	Charadriiformes	Procellariiformes	Pelecaniformes
Proximal end, tibiotarsus	*	×	–
Proximal end, femur	–	×	×
Pelvis	*	*	×
Vertebrae	*	×	–
Sternum, other than anterior facet	*	×	–
Anterior edge of carina	–	*	*
Coracoid	*	*	×

* very similar; × some similarity; – little or no similarity

Table 2

Comparison of cranial elements of *Prophaethon* with extant orders of birds

	Charadrii-formes	Procellarii-formes	Phaethon-tidae	other Pelecani-formes
Lower Mandible				
Shape	×	*	–	*
External intraramal suture area	*	*	×	–
Articulation	*	*	–	–
Posterior fossa	*	*	×	–
Prearticular	–	*	–	*
Skull				
Palate	*	×	–	–
Rostrum	*	–	–	×
Frontonasal hinge	*	–	*	×
Unfused prefrontals	*	–	*	*
Temporal fossae	*	×	*	*
Supraoccipital area	×	*	×	–
Quadrate articulation area	×	×	*	*

* very similar; × some similarity; – little or no similarity

IV. DISCUSSION AND CONCLUSIONS

From the above data comparing *Prophaethon* with Recent birds there would appear to be several possible hypotheses concerning its relationship to known taxa.

The species might be regarded as a charadriiform bird, showing the alcid type of pelvis and with a head adapted for catching prey in water and showing modifications which have parallels elsewhere in the taxon. But the specialized sternum with its facet for furcular attachment is not present in known Charadriiformes, and it would be necessary to argue that, since it is known in aquatic birds of two other orders, it might be an adaptation that potentially could have evolved under any similar behavioural or environmental selection pressures.

Prophaethon might be regarded as a procellariiform bird, in which case there is a precedent for a modified sternum, but the skull and rostral characters would not be typical of the known forms of that order.

If it is argued that the possession of both the specialized frontonasal hinge and the sternum are indications of pelecaniform affinities, then another assumption must be made, that a saltatory form of evolution has produced the more extremely evolved characters now present in this evolutionary diverse order while retaining more generalized characters in other structures which could presumably undergo subsequent modification. This is at variance with the apparent evidence provided by a proto-frigatebird from the Lower Eocene, described by Olsen (1974), which shows modifications in various skeletal elements of the postcranial skeleton but has not achieved either the specialized skull or the sternum typical of the Fregatidae.

If any of the above suggestions are adopted then, at least in so far as the early Tertiary is involved, the range of osteological characters used to define any of the three orders must be extended to include a number of significant characters which are at present regarded as diagnostic of some other order. The limiting groups of characters which may be used to assign any species to a particular order will then no longer be clearly separable ; we shall have to assume it is not possible to identify a bird from this geological period unless certain critical skeletal elements are available.

Alternatively, in view of the lack of evidence of affinity with any single order, it could be suggested that in the early Tertiary these three Recent orders had not yet diverged, and that *Prophaethon* was referable to an ancestral stem from which more than one Recent order had subsequently evolved. There is, however, a considerable amount of fossil bird material from this period, most of which appears to be referable to Recent families, suggesting that the degree of evolutionary divergence apparent in Recent families had already occurred by this period. In addition fossils referred to Pelecaniformes and Charadriiformes are known from the Upper Cretaceous and from the evidence available it seems that in general the ordinal divisions of birds had occurred within the Cretaceous.

Some other Lower Eocene species show this intermediacy of affinities. Among the more specialized forms described from this period is a sea-bird with bony, tooth-like projections on the jaws, *Odontopteryx toliapica* of the family Odontopterygidae. Related forms, usually separated in the family Pseudodontornithidae, are known from the Miocene. In recent studies of the British Lower Eocene we have found evidence of more numerous and varied forms of both families at this period. These birds were at first regarded as pelecaniform, but Howard (1957), in describing *Osteodontornis orri* of the Californian Miocene, pointed out that the skeleton showed a mixture of pelecaniform and procellariiform characters. The British specimens, recently prepared, appear to confirm the rather specialized nature of this group.

Avian phylogeny in the Cretaceous is still a mystery and in view of the lack of evidence speculation is of very limited use. If the Lower Eocene is taken as a base line there is an array of families known from fossil remains, most of them first known to occur at this period and subsequently persisting until Recent times. If we insert into this array both *Prophaethon* and the bony-toothed birds we may produce the kind of picture shown in simplified and linear form in Fig. 7.

Let us assume that the base line is the Lower Eocene and the lines rise to the Holocene, that A1–A3 represents charadriiform families, B1–B3 pelecaniform families and C1–C3 procellariiform families. If we insert *Prophaethon* as AB, the Odontopterygidae as BC1 and the Pseudodontornithidae as BC2, then we have a continuous sequence in which each family shares some characters with the adjacent ones and the whole presents a relatively uniform array which might have arisen as a complex adaptive radiation from a single ancestral origin, rather than as a divergence from three separate stems, yet showing some morphological convergence. If during later periods *Prophaethon* and the bony-toothed birds became extinct, then the remaining families would appear to fall into more discrete groups which are then identified as Recent orders – ordinal definition being aided by the absence of the intervening forms. The diagram presented is a linear one, but the relationships should be visualized as three-dimensional, the three Recent orders forming a triangle.

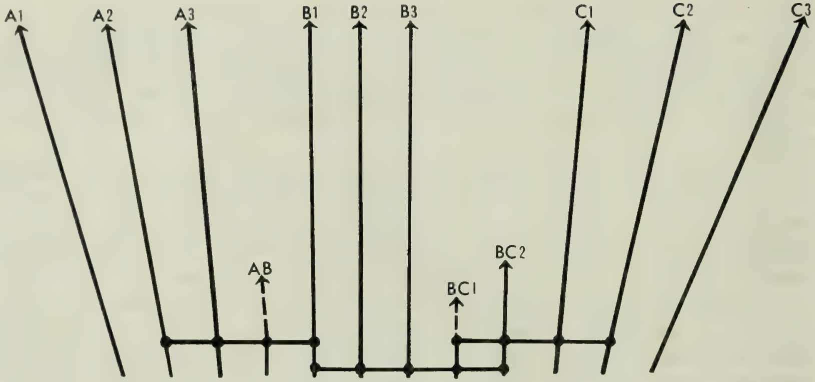


FIG. 7. Hypothetical relationship of families.

The bony-toothed birds would occupy the space intervening between the Pelecaniformes and the Procellariiformes, while *Prophaethon* would come in a more central position in view of its similarities to all three orders.

We have also indicated by transverse lines two possible distributions of shared characters resulting from the loss of some of these families. If BC1–2 disappear then the two linking characters which they share become discrete ordinal peculiarities. The character which AB is shown as sharing with families on either side would, following the extinction of AB, still persist in more than one Recent order but might be limited to certain families. If we assume A1–3 to be charadriiform families and B1 to be the Phaethontidae, species of the latter are seen to share a number of minor morphological characters with the former group and not with other pelecaniform families. The existence of such characters led to some early suggestions that the Phaethontidae had more affinity with the Charadriiformes than with the Pelecaniformes, and Mathews & Iredale (1921) created for it a suborder within their gull order, Lari. These similarities have also been explained as convergence with the terns (Sterninae of the Laridae) brought about by similar methods of feeding. The latter might be a valid explanation, but on the basis of the hypothesis proposed some at least of these similarities might be explained by a closer degree of affinity between the families involved at an earlier period and by the persistence of some shared characters.

This proposed arrangement would appear the most satisfactory to explain the combinations of characters found in *Prophaethon* and the bony-toothed birds, and to present a balanced view of sea-bird evolution in the Lower Eocene based on present evidence. There has for long been general acceptance that the pelecaniform and procellariiform birds shared a common ancestry more recent than that of avian orders in general. The suggested association of the Charadriiformes with these has been weaker and based mainly on the peculiarities shown by the Phaethontidae.

The evidence from the skeletal structure of *Prophaethon* might now justify, provisionally, a stronger linking of the Charadriiformes with the Pelecaniformes. These three Recent orders, with the two interordinal linking taxa, appear to form a more unified group, perhaps a single superorder which, for the purposes of arranging avian taxa of the Lower Eocene and earlier periods, might provide a more convenient unit than the existing groups.

This idea does not significantly conflict with present views on affinities based on the study of Recent taxa. These are summarized by Sibley & Ahlquist (1972) in their study of non-passerine relationships based on egg-white protein electrophoresis. There are various characters which appear to link the three Recent orders, and in addition the Gaviiformes are considered to be closely related to the Charadriiformes and the Sphenisciformes to the Procellariiformes. These two additional orders should perhaps be included in any proposed major grouping. Sibley & Ahlquist found evidence of similar starch gel egg-white patterns in Sphenisciformes, Gaviiformes, Procellariiformes, Charadriiformes, and possibly the Pelecanidae, Fregatidae and Phaethontidae. There is therefore evidence of a large and interrelated supraordinal group, within which some earlier links may still be undiscovered.

While this hypothesis may help to establish the position of *Prophaethon* within the framework of palaeontological phylogeny, the problem of fitting it into the existing taxonomic hierarchy still remains. As we have already indicated, it does not show definite affinity with any single existing taxon and to attempt to associate it with one of these would affect ordinal definitions based on osteology. From a nomenclatural point of view the alternative treatment of the specimen seems preferable whereby its isolated position is recognized. In terms of Recent taxonomy *Prophaethon* constitutes an interordinal link. For nomenclatural purposes it seems preferable to treat it as a monotypic order, Prophaethontiformes, with the single family Prophaethontidae, while recognizing its special character. It is then possible to insert it into the existing framework without unduly affecting existing taxa, and it can be merged with another taxon at a later date if new and overriding evidence should justify this. For the moment we would recommend that its placement should be between the Pelecaniformes and the Charadriiformes.

V. SYSTEMATIC DESCRIPTION

Order PROPHAETHONTIFORMES nov.

ORDINAL DIAGNOSIS. Dorsal surface of skull with prominent postorbital process and deep, rounded temporal fossae. Cranium small. Anterior lateral surface of frontal flattened for attachment of unfused prefrontal. Deep fronto-nasal hinge with prominent brow ridge. Lateral nasal struts lie alongside, and may fuse with, rostrum just anterior to hinge. Elongated, oval depression in roof of orbit bordering external edge. Zygoma laterally flattened with no dorso-ventral torsion at anterior end. Rostrum tapering evenly with nares approaching schizorhinal condition but terminating anterior to fronto-nasal hinge. Elongated nasal aperture extending almost to rostral tip. Palate typically schizognathous. Quadrate with large projecting flange on otic process, and posterior lower end of shaft with deep, narrow groove. Lower mandible long and slender. Dentary with horizontal external groove. Posterior mandibular fossa large, not perforating external wall. Prearticular large.

Carina of sternum deep, with curved ventral edge and anteriorly projecting apex with well-developed manubrial spine. Flattened anterior surface at carinal apex for articulation of furcula, and carinal tip bifurcated. Coracoid sulcus shallow with poorly-developed ventral lip. Ventral labial prominence projecting and rounded.

Coracoid with large sterno-coracoid surface, slightly curved ventrally, and sternal facet wide. Small facet for labial prominence on ventral surface. Procoracoid stout, projecting laterally and curving anteriorly. Coracoid fenestra present. Glenoid facet projecting dorso-ventrally.

Pelvis elongated and relatively narrow, with prominent median dorsal ridge, and narrow posterior shield between raised posterior iliac crests. Fused synsacrum with greatest depth at anterior end, tapering posteriorly. Last thoracic vertebra not fused to synsacrum. Anterior iliac plates sloping down steeply and curving outwards to form broad, lateral flanges which project a little anterior to end of the synsacrum.

Femur with internal cotylar surface internally deflected towards distal end. Proximal trochanter has abrupt obturator ridge with hollow on posterior side. Trochanteric ridge prominent.

Inner cnemial crest of tibiotarsus extending proximally well beyond anterior surfaces, as a thin flange projecting prominently, with some external curvature at outer edge. Outer cnemial crest thicker distally than inner crest, with proximal end terminating at an angle a little proximal to articulating surfaces. Internal articular surface with a posteriorly projecting curved lip.

Family **PROPHAETHONTIDAE** nov.

Diagnosis. The only family of its order.

Genus ***PROPHAETHON*** Andrews 1899

Diagnosis. The only genus of its family.

Type Species. *Prophaethon shrubsolei* Andrews.

Prophaethon shrubsolei Andrews 1899

(Pls 1–3 ; Figs 1–6)

1899 *Prophaethon shrubsolei* Andrews : 776–785, pl. 51.

Diagnosis. The only species of its genus.

Holotype. Imperfect skull, lower jaws and hyoids, sternum, right coracoid, distal end of left coracoid, left scapula, right femur, proximal end of left tibiotarsus, 11 vertebrae, rib fragments and synsacrum. In British Museum (Natural History), Department of Palaeontology registered number A683.

Locality and Horizon. Lower Eocene, London Clay (Ypresian) of Sheppey, Kent, England.

VI. ACKNOWLEDGMENTS

We wish to thank Mr F. M. P. Howie for preparing the specimen, Miss M. L. Holloway for making the detailed line drawings, and Mr F. Greenaway for taking the photographs.

VII. REFERENCES

Andrews, C. W. 1899. On the remains of a new bird from the London Clay of Sheppey. *Proc. zool. Soc. Lond.*, **1899** : 776–785 ; pl. 51.

Howard, H. 1929. The avifauna of the Emeryville shellmound. *Univ. Calif. Publs Zool.*, Berkeley, **32** : 301–394.

—— 1957. A gigantic 'toothed' marine bird from the Miocene of California. *Bull. Dep. Geol. S. Barbara Mus. nat. Hist.*, **1** : 1–23, 8 figs.

Jollie, N. T. 1957. The head skeleton of the chicken and remarks on the anatomy of this region in other birds. *J. Morph.*, Boston, Mass., **100** : 389–436, 26 figs.

Mathews, G. M. & Iredale, T. 1921. *A Manual of the Birds of Australia*, **1**. 279 pp. London.

Olsen, S. L. 1974. New fossil evidence of the origin of Frigatebirds. *Abstr. 16th int. orn. Congr.*, Canberra : 61–62.

Pycraft, W. P. 1898. Contributions to the Osteology of Birds. Part I. *Steganopodes*. *Proc. zool. Soc. Lond.*, **1898** : 82–101, pls 7–8, figs 1–8.

Sibley, C. G. & Ahlquist, J. E. 1972. A comparative study of the egg white protein of non-passerine birds. *Bull. Peabody Mus. nat. Hist.*, New Haven, Conn., **39** : 1–246, 37 figs.

VIII. INDEX

The page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

Alcidae 19–20, 22
Andrews, C. A. 3–4

bony-toothed birds 25–6
Burhinidae 21–2

carina 23
Charadriiformes 3, 18–27
Chionidae 22
Columbiformes 21
comparisons with Recent material 18–24
coracoid 4, 10*, 13–14, 17, 20–1, 23 ; pl. 2, figs D–G
cranial structures 4–8, 24
Cretaceous, ordinal divisions of birds within 25

Diomedea 18–19

egg-white protein electrophoresis 27
evolution of birds 24–7

families, hypothetical relationship of 25, 26*
femur 4, **15**, 18–19, 23
Fregatidae 20, 22, 24, 27

Galliformes 21
Gaviiformes 21–2, 27
Glareolidae 22
Greenaway, F. 29
Gruiformes 21–2

Haematopus 21
Holloway, Miss M. L. 29
Howie, F. M. P. 4, 29

Ibidorhynchus 21

jaw, lower, see mandible

Lari 26
Laridae 20–2, 26
Larus 19, 21
limb-bones 4 ; see femur, etc.

Macronectes 19
mandible, lower 4, **9–11**, 12*, 17, 21, 24 ; pl. 2, figs A–C
measurements 16–18

nasal structures 21–2
nostrils 4

Odontopterygidae 25
Odontopteryx toliapica 25
orbital structure 4–7
Osteodontornis orri 25

palate, 4, 7*, **8**–**9**, 21 ; pl. 1, fig. B
Pelecanidae 20, 27
Pelecaniformes 3, 6, 19–27
Pelecanoididae 20
pelvis 4, **14**–**15**, 18–19, 23 ; pl. 3, figs A–C
Phaethon 4, 19–23
Phaethontidae 3–4, 20, 22–4, 26–7
Phalacrocoracidae 20–2
Phalacrocorax 4, 19
Phoebetria 19
Pluvianus 22
Podicipitiformes 20–2
postcranial elements 11–16, 23
Procellariidae 21
Procellariiformes 3, 18–27
Prophaethon shrubsolei 1–29 *passim*, **28** ; pls 1–3
Prophaethontidae fam. nov. 27, **28**
Prophaethontiformes ord. nov. 3, **27**–**8**
proto-frigatebird 24
Pseudodontornithidae 25
Puffinus 19

quadrate **8**, 17

Rhynchops 22
ribs 4, **16**
rostrum **9**, 21–2

scapula 4, **14**, 17
Sheppey, Isle of 3
Shrubsole, W. H. 3
skull 3, **4**–**11**, 5*, 7*, 16–17, 21–4 ; pl. 1, figs A–E
Sphenisciformes 21, 27
Stercorarius 18, 22
Sterninae 26
sternum 4, **11**–**13**, 12*, 18, 20, 23
Sula 4, 19
Sulidae 20, 23

Thinicoridae 22
tibiotarsus 4, 12*, **16**, 18–19, 23; pl. 3, figs D–E

Uria 22

vertebrae 4, 19, 23

X-rays 4

Dr C. J. O. Harrison, Ph.D.
Subdepartment of Ornithology
British Museum (Natural History)
Tring
Herts

C. A. Walker
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Accepted for publication 18 July 1975

PLATE 1

Prophaethon shrubsolei Andrews

BM(NH) Pal. Dept. no. A683. Views of skull, × 1.

A. dorsal (p. 5)
B. ventral (p. 7, 8)
C. left lateral (p. 4)
D. right lateral (p. 4)
E. posterior (p. 7)

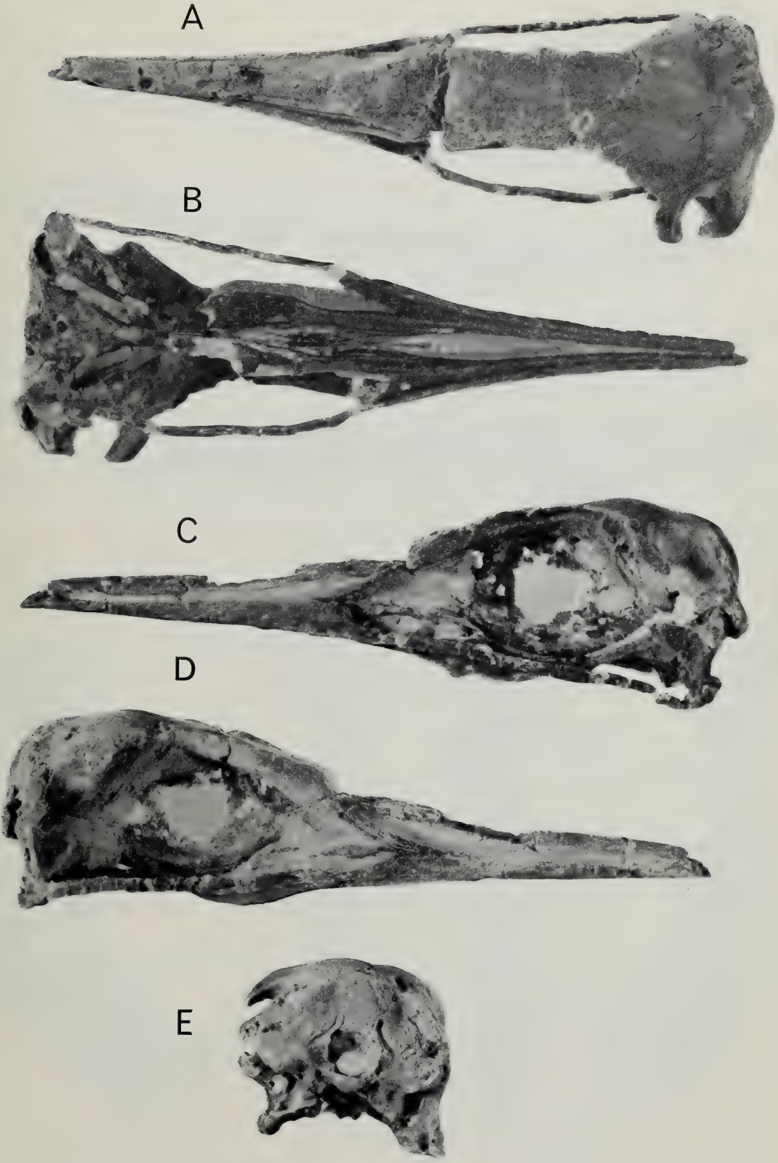

A
B
C
D
E

PLATE 2

Prophaethon shrubsolei Andrews

BM(NH) Pal. Dept. no. A683. Views of lower mandible, × 1. (p. 9)

- A. dorsal
- B. ventral
- C. left lateral

BM(NH) Pal. Dept. no. A683. Views of right coracoid, × 2. (p. 13)

- D. dorsal
- E. external
- F. internal
- G. ventral

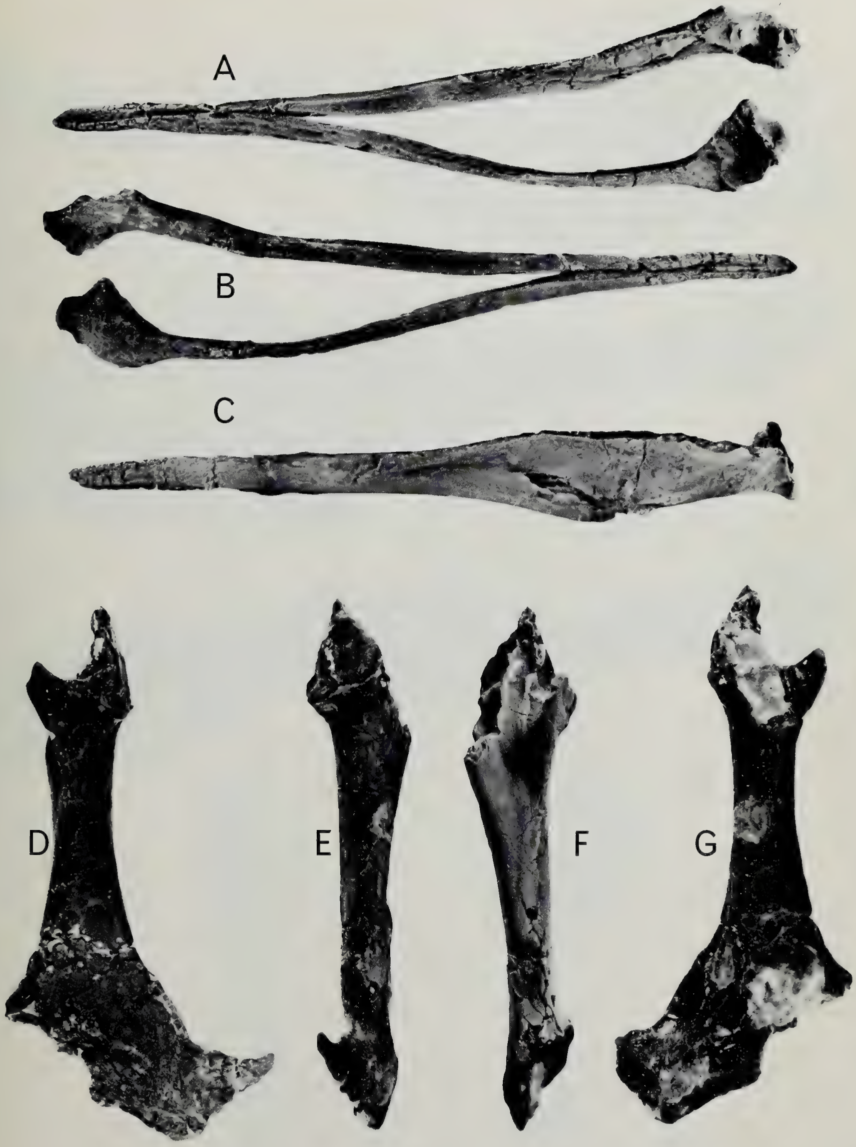

A
B
C
D
E
F
G

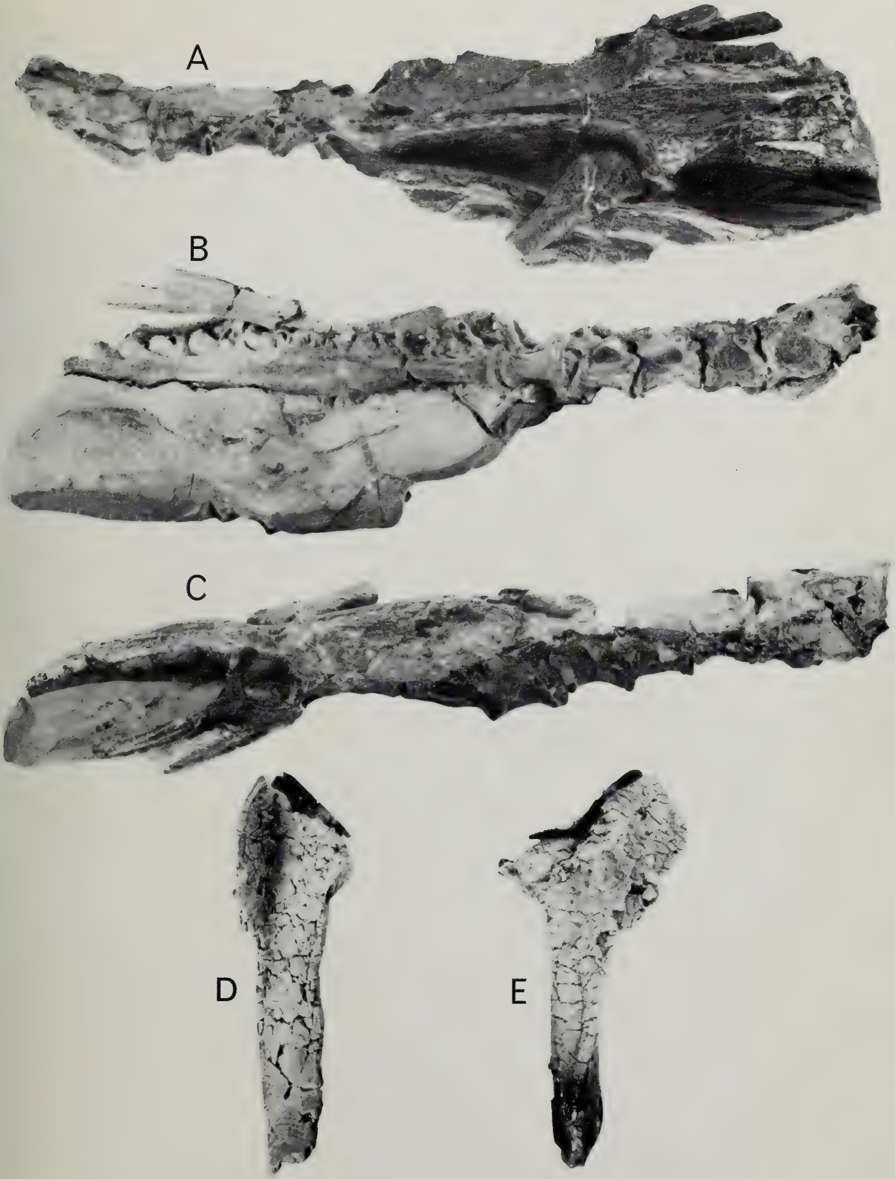
PLATE 3

Prophaethon shrubsolei Andrews

BM(NH) Pal. Dept. no. A683. Views of pelvis, × 1. (p. 14)
  A. dorsal
  B. ventral
  C. right lateral

BM(NH) Pal. Dept. no. A683. Views of proximal end of left tibiotarsus, × 2. (p. 16)
  D. anterior
  E. internal

PLATE 3



A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. Cox, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. OUT OF PRINT.
2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £11.
3. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £8.20.
3. Appendix. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.
4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 16 Text-figures. 1968. £6.10.
5. Rhodes, F. H. T., Austin, R. L. & Druce, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 313; 31 Plates; 92 Text-figures. 1969. £13.10.
6. Childs, A. Upper Jurassic Rhynchonellid Brachiopods from Northwestern Europe. Pp. 119; 12 Plates; 40 Text-figures. 1969. £5.25.
7. Goody, P. C. The relationships of certain Upper Cretaceous Teleosts with special reference to the Myctophoids. Pp. 255; 102 Text-figures. 1969. £7.70.
8. Owen, H. G. Middle Albian Stratigraphy in the Anglo-Paris Basin. Pp. 164; 3 Plates; 52 Text-figures. 1971. £7.20.
9. Siddiqui, Q. A. Early Tertiary Ostracoda of the family Trachyleberididae from West Pakistan. Pp. 98; 42 Plates; 7 Text-figures. 1971. £9.60.
10. Forey, P. L. A revision of the elopiform fishes, fossil and Recent. Pp. 222; 92 Text-figures. 1973. £11.35.
11. Williams, A. Ordovician Brachiopoda from the Shelve District, Shropshire. Pp. 163; 28 Plates; 11 Text-figures; 110 Tables. 1974. £12.80.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

SBM.0

PLEISTOCENE RODENTS OF THE BRITISH ISLES

GENERAL
29 JUL 1976
LIBRARY

A. J. SUTCLIFFE
AND
K. KOWALSKI

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 2
LONDON: 1976

PLEISTOCENE RODENTS OF THE BRITISH ISLES

GENERAL
JUL
LIBRARY

BY

ANTONY JOHN SUTCLIFFE
British Museum (Natural History), London

AND

KAZIMIERZ KOWALSKI
Institute of Systematic and Experimental Zoology,
Polish Academy of Sciences, Kraków, Poland

Pp. 31–147 ; 31 *Text-figures* ; 13 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 2
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 27, *No.* 2, *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 29 *July*, 1976 *Price* £7.40

PLEISTOCENE RODENTS OF THE BRITISH ISLES

By A. J. SUTCLIFFE & K. KOWALSKI

CONTENTS

Page

SYNOPSIS 35
I. INTRODUCTION 36
  A. HISTORY OF STUDIES 37
  B. THE GEOLOGICAL BACKGROUND 40
II. LOCALITIES IN THE BRITISH ISLES WITH FOSSIL RODENTS . . 42
  A. DEPOSITS OF EAST ANGLIA 42
    (i) Red Crag 43
    (ii) Icenian Crag 43
    (iii) Cromer Forest Bed Series 46
      (a) Pastonian of East Runton and Happisburgh . . 47
      (b) Beestonian 48
      (c) Cromerian, *sensu stricto* 48
      (d) Anglian 48
  B. TERRACE AND SOLIFLUXION DEPOSITS OF THE RIVERS THAMES AND LEA 48
    (i) Lower Thames 51
      (a) High Terrace of Swanscombe 51
      (b) Clacton 52
      (c) Early Middle Terrace at Aveley, Grays Thurrock and Ilford 53
      (d) Late Middle Terrace at Crayford and Erith . . 54
      (e) Floodplain Terrace complex 54
      (f) The Middle Terrace/Floodplain Terrace problem . 55
    (ii) Upper Thames 58
      (a) Isleworth 58
      (b) Marlow 58
    (iii) River Lea 58
      (a) Water Hall Farm Gravel Pit 58
      (b) Nazeing, Ponders End, Edmonton and Hackney . 59
    (iv) Solifluxion and melt-water deposits 59
      (a) Northfleet, Ebbsfleet and Baker's Hole . . 59
  C. CAVE DEPOSITS 60
    (i) Westbury Fissure 60
    (ii) Kent's Cavern 61
    (iii) Tornewton Cave 62
    (iv) Other caves with pre-'Ipswichian' deposits . . . 65
    (v) 'Ipswichian' cave deposits 67
    (vi) Caves with post-Ipswichian deposits 67
    (vii) Caves in Scotland 67
    (viii) Caves in Ireland 68
  D. OTHER LOCALITIES 69
    (i) Cromerian localities 69

Page

(ii) Hoxnian localities 69
(iii) 'Ipswichian' localities 69
(iv) Last Glaciation localities 69
(v) Holocene localities 72
(vi) Scottish localities 73

III. Classification and distribution of rodents in the Pleistocene of the British Isles 73
Family Sciuridae Brandt 73
Genus *Sciurus* Linnaeus 73
Sciurus whitei Hinton 73
Sciurus vulgaris Linnaeus 74
Genus *Spermophilus* Cuvier 75
Spermophilus (*Urocitellus*) *primigenius* Kormos 75
Spermophilus (*Colobotis*) *superciliosus* (Kaup) 76
Family Gliridae Thomas 77
Genus *Muscardinus* Kaup 77
Muscardinus avellanarius (Linnaeus) 77
Family Castoridae Gray 78
Genus *Trogontherium* Fischer 78
Trogontherium minus Newton 78
Trogontherium boisvilletti (Laugel) 78
Genus *Castor* Linnaeus 79
Castor fiber Linnaeus 79
Family Muridae Gray 81
Genus *Apodemus* Kaup 81
Apodemus sylvaticus (Linnaeus) 81
Apodemus flavicollis (Melchior) 83
Genus *Micromys* Dehm 84
Micromys minutus (Pallas) 84
Genus *Mus* Linnaeus. 84
Mus musculus Linnaeus 84
Genus *Rattus* Fischer. 84
Rattus rattus (Linnaeus) 84
Rattus norvegicus (Berkenhout) 84
Family Cricetidae Rochebrune 85
Genus *Cricetus* Leske. 85
Cricetus cricetus (Linnaeus) 85
Genus *Allocricetus* Schaub 86
cf. *Allocricetus bursae* Schaub 86
Genus *Dicrostonyx* Gloger 87
Dicrostonyx torquatus (Pallas) 87
Genus *Lemmus* Link 90
Lemmus lemmus (Linnaeus) 90
Genus *Clethrionomys* Tilesius 92
Clethrionomys glareolus (Schreber) 92
Genus *Pliomys* Méhely 95
Pliomys episcopalis Méhely 95
Genus *Mimomys* Major 95
Mimomys pliocaenicus Major 95
Mimomys reidi Hinton 97
Mimomys newtoni Major. 97
Mimomys savini Hinton 98

Page
Genus *Arvicola* Lacépède 99
Arvicola cantiana (Hinton) 102
Arvicola cantiana-terrestris 103
Arvicola terrestris (Linnaeus) 103
Genus *Pitymys* McMurtrie 105
Pitymys arvaloides Hinton 106
Pitymys gregaloides Hinton 107
Genus *Microtus* Schrank 107
Microtus arvalinus Hinton 108
Microtus agrestis (Linnaeus) 109
Microtus arvalis (Pallas) 112
Microtus nivaloides Major 114
Microtus nivalis (Martins) 114
Microtus ratticepoides Hinton 116
Microtus oeconomus (Pallas) 117
Microtus gregalis (Pallas) 118
Genus *Lagurus* Gloger 120
Lagurus lagurus (Pallas) 120

IV. HISTORY OF THE RODENT FAUNA OF THE BRITISH ISLES DURING THE PLEISTOCENE 121
Red Crag 122
Icenian Crag and Pastonian Forest Bed 122
Cromerian *sensu stricto* 122
'Westbury stage' 122
Mundesley Arctic Bed 123
Hoxnian deposits 123
Comparison of the rodent faunas 123
Notes on the Wolstonian-Ipswichian part of the succession . 124
Middle Terrace of the Thames interglacial 125
Tornewton Cave Glutton Stratum cold stage 125
Joint Mitnor interglacial 126
Last Glaciation 127
Holocene 128
Ireland 129

V. ACKNOWLEDGEMENTS 129

VI. REFERENCES 130

VII. INDEX 137

SYNOPSIS

For nearly half a century, since its publication in 1926, M. A. C. Hinton's *Monograph of the Voles and Lemmings* has remained the only comprehensive work on British Pleistocene rodents. Subsequent advances in Quaternary studies and the availability of new fossil material have made some updating of this publication necessary. In the present work a brief historical review of the studies of British Pleistocene rodents is followed by a description of the rodent assemblages from the principal fossil localities. Rodent species recorded from the British Pleistocene are then discussed in systematic order and, finally, an attempt is made to relate a generalized sequence of rodent faunas to the climatic sequence usually employed today as the basis for British Pleistocene chronology.

I. INTRODUCTION

NEARLY half a century has elapsed since the publication by the British Museum (Natural History) of M. A. C. Hinton's *Monograph of the Voles and Lemmings* in 1926. Today it is still the only comprehensive work on British Pleistocene rodents and remains the standard reference work on this subject. In the meantime there have been great advances in many related fields of study. Hinton did not attempt to relate his sequence of rodent faunas to the glacial–interglacial sequence of climatic events, which was already gaining favour at the time of his studies, and which is known today to be even more complicated than the four glacial and three interglacial stages for so long employed as a basis of Pleistocene chronology.

Excavations in the British Isles since 1926 have produced a wealth of new fossil rodent material which was not available to Hinton. Findings from the Westbury-sub-Mendip Fissure (Somerset), Swanscombe (Kent), Tornewton Cave (Devon) and a series of Late Glacial cave sites in the Peak District (Staffordshire and Derbyshire), excavated and published by various workers, are of special importance. The advent of carbon-14 (^{14}C) dating has permitted the accurate dating of some Upper Pleistocene rodent remains. Studies of pollen and insects are further, relatively new, stratigraphic aids.

On the continent of Europe there have been great advances in rodent studies which provide a basis for the interpretation of rodent migrations into the British Isles and assist in identifying stages of geographical isolation. W. von Koenigswald's recent work (1972, 1973) on the *Mimomys–Arvicola* lineage, based initially on continental European remains and subsequently extended to the British Isles, throws new light on the British Pleistocene rodent sequence.

In the present work the authors have cooperated on a reappraisal of the Pleistocene rodent faunas of the British Isles. One of us (K. Kowalski of Kraków, Poland) is mainly responsible for the systematic part and for comparison with continental evidence; the other (A. J. Sutcliffe of London) for the stratigraphic sequence of British rodent faunas. Discussions with W. von Koenigswald (Tübingen) about the *Mimomys–Arvicola* lineage have contributed fundamentally to the last-mentioned part of this work.

Although we cover 37 species of rodents from over 100 sites, many problems remain which can only be resolved by further careful collecting. Additional material is needed from critical deposits such as the early and late parts of the Forest Bed Series of Norfolk and from Hinton's Middle Terraces of the Thames, or from deposits of equivalent age. Some of the faunal assemblages which we have listed, such as that from the Otter Stratum of Tornewton Cave, are unique and cannot be compared with deposits of the same age in other parts of the British Isles. We have shown scarcely any evidence of differences between contemporary faunas in different areas, nor of temporal faunal changes within the broad climatic phases used for reference. The systematic relationship between some of the rodent species is still far from clear. All these aspects of rodent studies and many others offer great scope for future research. If this Bulletin provides a stepping stone for such work it will have been worth while.

A. History of Studies

Although publications of the eighteenth century and, in greater number, of the first decades of the nineteenth contain references to the occurrence of remains of beaver in British Quaternary deposits, the first scientific description of fossil rodents from this country did not appear until the middle of the nineteenth century. In 1846 R. Owen published a detailed description, accompanied by excellent drawings, of the remains of *Trogontherium cuvieri* and *Castor fiber* from the Forest Bed deposits of East Anglia. He also mentioned the presence of the remains of *Arvicola* 'which I have been unable satisfactorily to distinguish from *Arvicola amphibia*, or common Water-rat' (1846 : 202) in the sediments of many caves. The bones of the same species were present, according to Owen 'in newer pliocene deposits'. He considered (1846 : 205) the specimens from the 'older pliocene crag near Norwich . . . indicated a species of *Arvicola* intermediate in size between the Water-vole (*Arvicola amphibia*) and the Field-vole (*Arvicola arvalis*)'.

The next important contribution to the study of British Pleistocene rodents was that of W. A. Sanford. His papers on rodents from caves of Somerset (1870a, b) contain not only descriptions of forms still living in Britain (*Arvicola terrestris, Clethrionomys glareolus* and *Microtus agrestis*) but also of species now extinct in this country (*Microtus oeconomus, Lemmus* 'of the type of *L. norvegicus*' and *Dicrostonyx torquatus*). It is interesting to note that Sanford correctly determined the skulls of *D. torquatus* but ascribed jaws of the same species to *Arvicola gulielmi*. He mentioned also the occurrence of a small hamster, '*Cricetus songarus* (Pallas)', and *Spermophilus erythrogenoides*, a species previously discovered and described by H. Falconer (in Murchison 1868).

The first attempt to make a systematic classification of fossil voles, one of the most difficult groups of rodents, was made by H. P. Blackmore & E. R. Alston (1874). They failed to recognize the difference between Recent and fossil species, but were the first to record *Microtus nivalis* in Britain.

A series of works on the 'preglacial' deposits of East Anglia by E. T. Newton (1881, 1882a, b, 1890b, 1891 and 1909) provides an important contribution to the knowledge of the rodents of this area. Newton was the first to state that the vole remains were specifically different from Recent forms and he named a new species, *Arvicola intermedius* Newton 1881. He also published diagnoses of two other new species of rodents, a hamster, '*Cricetus vulgaris Runtonensis* n. subsp.' and a beaver '*Trogontherium minus* n. sp.' His work is of importance in regarding the vertebrate remains, including many rodents, from the 'pre-glacial' deposits of East Anglia as specifically distinct from living forms. He also published the first scientific description (1894, 1899a, b) of the vertebrate remains, including rodents, from the rich late Pleistocene fauna of Ightham Fissures, Kent.

The greatest contribution to the study of British Pleistocene rodents was that of M. A. C. Hinton (1883–1961). His first note on this subject appeared in 1900 and later this group of mammals became the main object of his interest. His work culminated in 1926 with the publication of volume 1 of his *Monograph of the Voles and Lemmings*. Hinton soon became the world authority on Microtinae and his monograph (unfortunately unfinished) is still the standard work in this branch of mammalogy. He was the first to recognize that, since rodent species have short ranges in time, their remains are of special stratigraphic value in the study of the Pleistocene. They thus help the geologist attempting to correlate scattered or isolated cavern deposits with others to which ordinary stratigraphical methods can be applied. The importance of this concept was further expanded by Kowalski (1966).

Hinton (1926a ; 1926b : 126–136) recognized a series of rodent faunas of different ages at British localities. In order of increasing antiquity these were as follows :

Third Terrace of the Thames, in the valley of the River Lea.
Ightham Fissure (Kent) stage.
Late Middle Terrace of the Thames (typical locality Crayford and Erith, Kent).
Early Middle Terrace of the Thames (typical locality Grays Thurrock, Essex).
High Terrace of the Thames (Ingress Vale, Swanscombe, Kent).
Upper Freshwater Bed at West Runton, Norfolk.
Shelly Crag at East Runton, Norfolk.
Norwich Crag and Weybourne Crag of the Norfolk Coast.

Although Hinton did not attempt to relate this division to any sequence of climatic fluctuations, his faunal stages were far ahead of any other palaeontological division of the British Pleistocene at that time.

Hinton also laid the basis for systematic study of the Microtinae (Savage 1963). After 1926 he abandoned nearly completely his study of the British fossil rodents, being involved in problems of pest control and the study of other mammals. He nevertheless published in 1952 a thorough description of rodent remains from the Late Glacial deposits of the Lea Valley.

Hinton's work is not only an important chapter in the history of zoology, but it still forms the standard reference on British Pleistocene rodents. For this reason it seems necessary to mention some of its limitations. He was a monoglacialist, or strictly an antiglacialist, as he postulated only one very late and only moderately cold period in the Pleistocene history of England. This opinion, which he regarded as the established truth, probably also influenced his zoological views. When he came across the fossil remains of species associated today with arctic climate he was inclined to determine them as forms different from Recent ones, since they could not then be used as evidence of particular climatic conditions.

Hinton was a prominent typologist. Although he was not more of a 'splitter' than most of his contemporary zoologists, he nevertheless used subspecific names extensively and was inclined to determine each new variant as a new species. For this reason, even in Hinton's own collection, many intermediate specimens were left undetermined.

Finally, Hinton accepted the multituberculate origin of rodents, a theory now generally rejected. He accepted that microtine evolution has always led from forms with complicated to forms with simple teeth. Strangely enough this did not hinder him in the correct reconstruction of some of the lines of evolution in voles, since among the different tendencies in the late evolution of the teeth of this particular group some lines did indeed progress from more complicated to simpler tooth-patterns.

Relatively few contributions to the study of British Pleistocene rodents have been published since the appearance of Hinton's monograph. These include the work of J. W. Jackson (1932, 1934); L. S. Palmer (1934); A. Schreuder (1929, 1931, 1950, 1951); J. N. Carreck (1957, 1966); D. Bramwell (1960, 1964, 1970); A. J. Sutcliffe & F. E. Zeuner (1962); J. C. Pernetta (1966); R. J. G. Savage (1966); K. Kowalski (1967); W. von Koenigswald (1973) and M. Bishop (1974, 1975). Most of these papers contain site lists of rodents with relatively little general discussion of their stratigraphical or systematic position. The papers by Schreuder (1929, 1931, 1951) are worthy of special mention for containing a thorough redescription and systematic discussion of the beaver remains from Britain. The paper of 1950 contains a list of the voles from the stratigraphically important Middle Pleistocene deposits of Swanscombe, Kent. More recently A. J. Stuart, in a general review of the British Pleistocene fauna (1974), listed the rodent faunas from key sites and discussed their stratigraphical occurrence.

Since the last synthetic work of Hinton (1926b) there has been great progress in other fields of study related to the problem of the history of British rodents. Investigations on the continent of Europe (not without influence from Hinton's work) have brought to light many rich local rodent faunas of Pliocene and Pleistocene age and have made it possible to reconstruct in greater detail the stratigraphical position and evolutionary history of many of these mammals. Recent contributions in the field include the work of J. Chaline (1972), who gives a detailed description of the rodents of the Middle and Upper Pleistocene of France, and of W. von Koenigswald, who studied the phylogenetic lineage of the genus *Arvicola*. In addition, knowledge of the systematic position, ecology and geographical variability of Recent rodents has greatly improved throughout the whole of the Palaearctic region.

In the British Isles there have been extensive geological and palaeobotanical studies (e.g. West 1968), which have provided a more detailed stratigraphic background for rodent studies. In addition the stratigraphic position of many old localities has been clarified and new rodent localities have been discovered. A new aspect of investigation has been provided by zoological studies of insular races of small mammals (Corbet 1961).

In view of the increasing importance of rodents in stratigraphic studies and of all the additional information which has become available since the publication of Hinton's monograph, it is timely to review the existing data on British Pleistocene rodents. In the description which follows the stratigraphic age of crucial rodent localities of the British Isles will be further examined, the systematic position and synonymy of the rodent species, currently overburdened with too many names connected with insufficiently characterized forms, will be discussed and the history of the rodent population of Britain during the Pleistocene reviewed. Many gaps nevertheless remain in the known sequence of events. This paper does not contain morphological descriptions of the various species of British Pleistocene rodents, a task, important for further stratigraphic and systematic studies, which needs to be carried out in the future. In the meanwhile subspecific designations are not used in the present paper. The nomenclature of living species of rodents here used is based mainly on the work of Ellerman & Morrison-Scott (1966). Information about morphology, biology and distribution of Recent rodents in Britain is available in Miller (1912), Matthews (1952), Southern (1964) and Corbet (1966). Beirne (1947) has discussed the possible arrival dates of some species of rodents into the British Isles.

B. The Geological Background

As previously mentioned, great progress has been made towards a more detailed understanding of the British Pleistocene sequence since Hinton published his monograph in 1926. Some deposits considered to be Pliocene at that time are now regarded as Lower Pleistocene, and there now exists a detailed picture, still being further elaborated from current studies, of alternating glacial and interglacial stages in the British Isles. A recent contribution of special importance is that of West & Wilson (1966), who demonstrated from palaeobotanical studies that the Cromer Forest Bed Series of Norfolk in fact represents two interglacial stages with an intervening cold stage.

At the present time the most generally accepted correlation for the British Pleistocene is that recommended by the Geological Society of London (Mitchell *et al.* 1973), which is shown, with some additional information from other sources indicated, in Table 1.

While in general it seems possible to relate most British rodent faunas to this sequence, there are some parts (notably the Cromerian and Wolstonian–Ipswichian stages) which seem inadequate to account for all the rodent stages currently attributed to them. There can be little doubt that they are more complex than is indicated in the table opposite.

Although, in the 1973 correlation of the Geological Society, the Wolstonian and Ipswichian are recognized as two stages only, an earlier correlation published by the same Society (Evans 1971) proposed a more detailed chronology for this part of Pleistocene time which must be mentioned here, since it has important application to our rodent studies.

From a consideration of information derived from deep-sea cores and other lines of evidence Evans argued that there had been more than one warm phase since the Hoxnian (Holsteinian) Interglacial. Whilst accepting the period from about 100 to 70 thousand years ago (which he regarded as the true Last Interglacial, the Ipswichian or Eemian, equivalent to Zeuner's Late Monastirian shoreline) as the only fully warm period of considerable length since the Holsteinian, he drew attention to other lesser mild phases of post-Holsteinian age about 170 000 and 130 000 years ago, possibly equivalent to the Danish Vejlby I and Vejlby II mild stages, the possible relationship of which is shown in Table 2.

Evans also drew attention to some problems related to the interpretation of this part of the Pleistocene sequence. He pointed out that Zeuner, who regarded the Last Interglacial as double, used the term 'Last Interglacial' for two different ranges of time, that lasting from 180 to 120 thousand years ago (cycles 5w and 4) and also for that lasting from 130 to 70 thousand years ago (cycles 4w and 3). He considered that some confusion had arisen in archaeological circles where 'Last Interglacial' had been used as a reference datum and preferred to restrict this term only to zone 3w.

TABLE 1

Generalized British Pleistocene sequence

	Stages: NW Europe	Stages: S Britain	Climate: Britain	British deposits	Hinton's Rodent Faunas (1926) Probable stratigraphic position
HOLOCENE	Holocene	FLANDRIAN	Temp.	CAVE TERRACE & ALLUVIAL DEPOSITS	
UPPER PLEISTOCENE	Weichselian	DEVENSIAN	Cold (G+P)		Third Terrace of the Thames in the Lea Valley Ightham Fissure Stage
	Eemian	IPSWICHIAN	Temp.		Late Middle Terrace of the Thames Early Middle Terrace of the Thames
	? Saalian (pars)	WOLSTONIAN (GIPPINGIAN)	Cold (G+P)		
MIDDLE PLEISTOCENE	Holsteinian	HOXNIAN	Temp.		High Terrace of the Thames
	? Saalian ? Elsterian	ANGLIAN (LOWESTOFTIAN)	Cold (G+P)		(Hinton's Plio-Pleistocene boundary)
		CROMERIAN	Temp.	CROMER FOREST BED SERIES	Upper Freshwater Bed at West Runton
LOWER PLEISTOCENE	'Cromerian'	BEESTONIAN	Cold (P)		
	Menapian	PASTONIAN	Temp.	ICENIAN CRAG (WEYBOURNE & NORWICH CRAGS)	Shelly Crag at East Runton
	Waalian	BAVENTIAN	Cold (P)		Norwich and Weybourne Crags
	Eburonian	ANTIAN	Temp.		
	Tiglian (U. Villafranchian of Italy)	THURNIAN	Cold		
	– – ? – –	LUDHAMIAN	Temp.	RED CRAG	
	Pre-Tiglian (L. Villafranchian of Italy)	WALTONIAN		(erosion)	
PLIOCENE	Reuverian (Astian of Italy)		Temp.	CORALLINE CRAG	

Based on West 1968, Sparks & West 1972, and Mitchell, Penny, Shotton & West 1973. Hinton's rodent stages (1926) are shown at their most likely position in the last column of the table. (Under Climate: Britain, G = Glacial, P = Periglacial.)

TABLE 2

Possible relationship of continental climatic divisions to British mild phases (after Evans 1971)

Evans' half-cycles (c = cold, w = warm)	Years ago	British stage names	Continental climatic divisions	Mediterranean sea levels
2c	70 000		Early Weichsel, Early Würm	
3w	100 000	IPSWICHIAN	Eemian	Late Monastirian
3c	120 000		Saale 2, Riss 2, Warthe	
4w	130 000		Vejlby 2	Main Monastirian
4c			Minor cold phase	
5w	180 000		Vejlby 1, ? Domnitz	
5c	200 000		Saale 1, Riss 1	
6w		HOXNIAN	Holsteinian	

It follows from Evans' chronology that the terms Saale 2, Riss 2 and Penultimate Glaciation of some authors have been used for periods of time later than Last Interglacial of some other authors, and that great confusion can arise here if stage names such as these are applied incautiously to our studies of British Pleistocene rodents. Likewise the terms Penultimate Glaciation or Wolstonian (when applied away from the type locality) could confusingly be used to mean any period of time from that considered by some writers to be the middle of the Hoxnian/Holsteinian (for example, Mullender's suggestion in Wymer (1974) that the upper part of Lower Loam of Swanscombe is Wolstonian) to that immediately preceding Evans' Interglacial half-cycle 3w. Wymer (1974) has suggested a warm stage during the Wolstonian. Bristow & Cox (in Mitchell *et al.* 1973) have argued, from their study of glacial deposits in East Anglia, that the interglacial deposits at the Hoxnian type locality of Hoxne belong to the last and not penultimate interglacial and they referred the Ipswichian and Hoxnian deposits, which they accepted may have been separated by a cold oscillation, to a single interglacial between the Devensian and Anglian.

In the present paper we will try to overcome such problems, as far as possible, by concentrating on establishing a relative chronology for the rodent faunas of the British Isles which will not be affected by future refinements in the naming of the British Pleistocene sequence, rather than to attempt to refer these faunas too rigidly to a chronology which is clearly incomplete. Let us now make a detailed examination of the rodent faunas from the various British Pleistocene localities.

II. LOCALITIES IN THE BRITISH ISLES WITH FOSSIL RODENTS

Remains of Pleistocene rodents have been found at many localities in the British Isles, notably in the early Pleistocene marine Crag and Forest Bed deposits of East Anglia and in later river terrace and cave deposits. In Ireland they are known only from cave deposits of late Pleistocene age. The location of the principal localities is shown in Fig. 1.

A. Deposits of East Anglia

Extensive areas of Suffolk and Norfolk are covered by Crag and Forest Bed deposits from which rodent remains have sometimes been recovered.

Although recent research (West & Wilson 1966, Norton 1967, West 1968) has greatly increased understanding of the early Pleistocene sequence of East Anglia, all the rodent remains from this region available for the present study are unfortunately from old collections, many of them with imprecise stratigraphic information. A series of rodent faunas can nevertheless be distinguished.

(i) RED CRAG. This is a marine shallow-water shore deposit typically laid down in land-locked bays. It is best developed in Suffolk where it consists mainly of shelly sands. There is also a basal nodule bed with rolled and polished fossils, including mastodon teeth, apparently derived by the Crag sea from earlier deposits. The occurrence of these derived fossils, which include mammalian remains of Eocene, Miocene and Pliocene age, makes the study of the Red Crag mammalian fauna extremely difficult. For a long time the deposit was considered to be of Pliocene age and it was not until 1948 that its Lower Pleistocene date was accepted and the occurrence of relatively unmineralized contemporary mammalian remains, associated with the derived fossils, was recognized.

Only a few rodent remains have been found in the Red Crag. *Trogontherium minus* (known from Astian localities on the European continent) and *Hystrix*, represented by teeth (Spencer 1966) and by gnawing on part of a deer antler (Sutcliffe & Collings 1972), are probably derived from pre-Pleistocene deposits and cannot be included in the contemporary Red Crag faunal list.

Castor fiber, recorded from a number of Red Crag localities, including Sutton and Woodbridge (47, Fig. 1) is probably a contemporary species. A rolled microtine tooth from the Red Crag has been provisionally referred by Spencer (1964) to *Mimomys* sp.

(ii) ICENIAN CRAG. A further series of marine deposits, the Icenian Crag (including the Norwich and Weybourne Crags), occupies a basin on the north of the Red Crag outcrop. It was apparently laid down in a more open sea. Its exact relationship to the Red Crag is not fully understood, but its age appears to range from Thurnian, through Antian and Baventian, to Pastonian. According to West (1968), these stages may be equivalent to the Tiglian, Eburonian and Waalian in the stratigraphy of the Netherlands. The relationship between the Norwich and Weybourne Crags is also not clear. The Weybourne Crag, typified by the mollusc *Macoma balthica*, is found at more than one stage. The youngest part of the sequence, including part of the Weybourne Crag, is of Pastonian age and is contemporaneous with the lowest part of the Cromer Forest Bed series. Part of the Norwich Crag of Suffolk may also be Pastonian.

Rodent remains, which have been found in the Norwich and Weybourne Crags of Bramerton (55, Fig. 1), Covehithe (51), Easton Bavents (50), Sizewell (49),Thorpe (48), Trimingham (61) and other localities represent *Mimomys pliocaenicus*, *M. reidi*, *M. newtoni*, *Castor fiber* and *Trogontherium boisvilletti*. Since conditions were unsuitable for the preservation of very small remains, it is not surprising that no teeth of glirids and murids have been found in the deposits. *M. pliocaenicus* and *M. reidi* are typical Tiglian (Upper Villafranchian) elements and confirm a Lower Pleistocene age for at least part of this series.

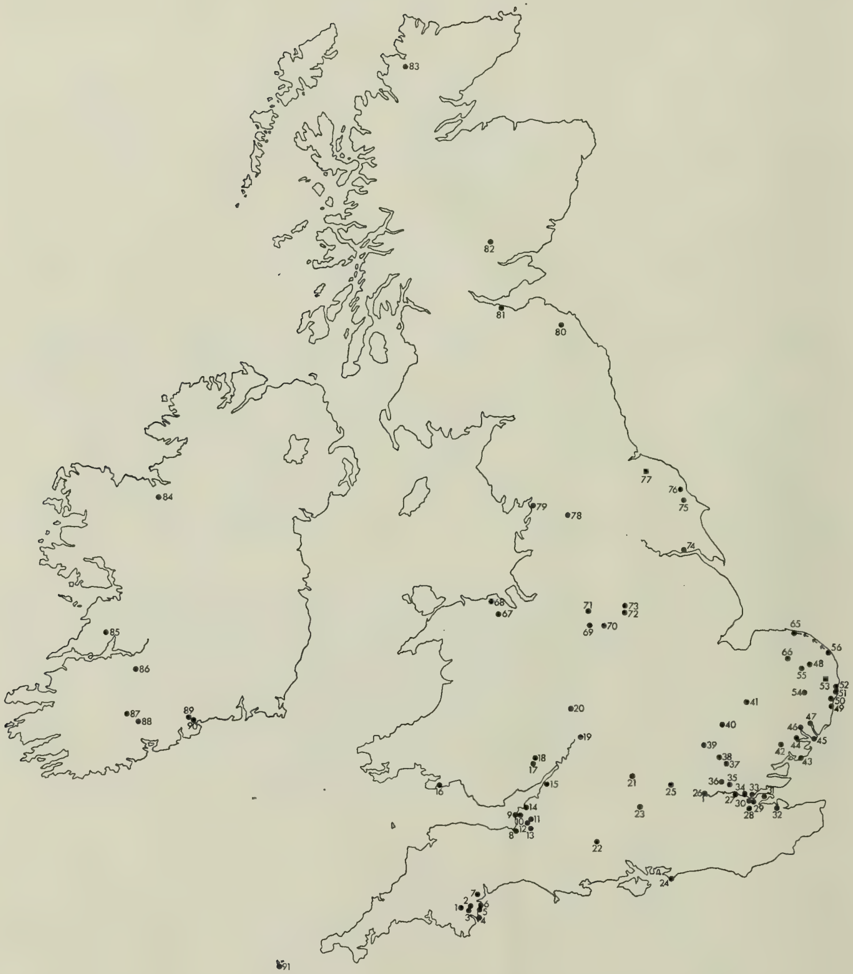

83
82
81
80
84
79
78
77
76
75
74
68
67
71
73
72
69
70
85
86
87
88
89
90
65
66
56
48
55
53
52
51
50
49
54
41
47
46
45
44
42
43
40
39
38
37
20
19
18
17
16
15
21
25
36
35
26
34
33
31
27
30
29
28
32
14
9
10
11
12
8
13
23
22
24
7
2
1
6
5
3
4
91

FIG. 1. Location map of the principal Quaternary rodent localities in the British Isles. Key to numbers opposite.

KEY TO FIG. I

1	Joint Mitnor Cave, Buckfastleigh, Devon
2	Levaton Cave, Torbryan, Devon
3	Tornewton Cave, Torbryan, Devon
4	Brixham Cave, Brixham, Devon
5	Happaway Cave, Torquay, Devon
6	Kent's Cavern, Torquay, Devon
7 (i)	Cow Cave, Chudleigh, Devon
7 (ii)	Chudleigh Fissure, Devon
8	Huntspill Cut, Huntspill, Somerset
9 (i)	Brean Down, nr Brean, Somerset
9 (ii)	Uphill Cave, Uphill, Somerset
10 (i)	Hay Wood Rockshelter, Hutton, Somerset
10 (ii)	Bleadon Cave, Bleadon, Somerset
10 (iii)	Picken's Hole, nr Bleadon, Somerset
10 (iv)	Hutton Cave, Hutton, Somerset
10 (v)	Banwell Cave, Somerset
11 (i)	Rowberrow Cavern, Burrington, Somerset
11 (ii)	Aveline's Hole, Burrington, Somerset
12	Gough's Cave, Cheddar, Somerset
13	Westbury-sub-Mendip Fissure, Somerset
14	Clevedon Cave, Clevedon, Somerset
15	Alveston Fissure, Alveston Gloucestershire
16 (i)	Minchin Hole, nr Penard, Glamorganshire
16 (ii)	Bacon Hole, nr Penard, Glamorganshire
17 (i)	King Arthur's Cave, nr Whitchurch, Herefordshire
17 (ii)	Great Doward Cave, Whitchurch, Herefordshire
18	Merlin's Cave, Symond's Yat, Herefordshire
19	Beckford, Worcestershire
20	Upton Warren, nr Droitwich, Worcestershire
21	Sugworth, Oxfordshire
22	Fisherton, Salisbury, Wiltshire
23	Thatcham, Berkshire
24 (i)	West Wittering, Sussex
24 (ii)	Selsey, Sussex
25	Marlow, Buckinghamshire
26	Isleworth, Middlesex
27	Crayford and Erith, Kent
28	Ightham Fissures, Ightham, Kent
29	Northfleet, Kent
30	Swanscombe, Kent
31	Upnor, Kent
32	Murston, Kent
33	Grays Thurrock, Essex
34	Aveley, Essex
35	Ilford, Essex
36 (i)	Hackney, London
36 (ii)	Angel Road, Middlesex (north London)
36 (iii)	Ponders End, Middlesex
37	Nazeing, Lea Valley, Essex
38	Water Hall Farm, Hertfordshire
39	Hitchin, Hertfordshire
40	Barrington, Cambridgeshire
41	Cambridge Fens (including Burwell and Swaffley), Cambridgeshire
42	Copford, nr Colchester, Essex
43	Clacton, Essex
44 (i)	Harkstead, Suffolk
44 (ii)	Stutton, Suffolk
45	Felixstowe, Suffolk
46 (i)	Bobbitshole, nr Ipswich, Suffolk
46 (ii)	Stoke Tunnel Beds, Ipswich, Suffolk
47 (i)	Sutton, Suffolk
47 (ii)	Woodbridge, Suffolk
47 (iii)	Kyson, Suffolk
48	Thorpe, Norfolk (see p.96)
49	Sizewell, Suffolk
50	Easton Bavents, Suffolk
51	Covehithe, Suffolk
52	Kessingland, Suffolk
53	Geldeston, nr Beccles, Norfolk
54	Hoxne, nr Diss, Suffolk
55	Bramerton, Norfolk
56	Happisburgh, Norfolk
57	Ostend, Norfolk
58	Bacton, Norfolk
59	Paston, Norfolk
60	Mundesley, Norfolk
61	Trimingham, Norfolk
62	Overstrand, Norfolk
63	Cromer, Norfolk
64	East Runton, Norfolk
65	West Runton, Norfolk
66	Swanton Morley, Norfolk
67	Lynx Cave, Denbighshire (exact location not known)
68	Gwaenysgor Cave, Prestatyn, Flintshire
69	Elder Bush Cave, Wetton, Staffordshire
70	Harborough Cave, Brassington, Derbyshire
71 (i)	Fox Hole Cave, High Wheeldon Hill, Earl Sterndale, nr Buxton, Derbyshire
71 (ii)	Etches' Cave, Dowel Dale, Earl Sterndale, nr Buxton, Derbyshire
71 (iii)	Dowel Cave, Dowel Dale, Earl Sterndale, nr Buxton, Derbyshire
72	Langwith Cave, Upper Langwith, nr Scarcliffe, Derbyshire
73	Pin Hole Cave, Creswell, Derbyshire
74	Hessle, nr Kingston-upon-Hull, Yorkshire
75	Staple Howe, nr Wintringham, Yorkshire
76	Star Carr, nr Scarborough, Yorkshire
77	Kirkdale Cave, Helmsley, Yorkshire
78	Cowside Cave No. 3, Settle, Yorkshire
79	Dog Holes Cave, Warton Crag, nr Carnforth, Lancashire
80	Middlestots Bog, Edrom Parish, Berwickshire, Scotland
81	Corstorphine, nr Edinburgh, Midlothian
82	Loch of Marlee, Kinlock, Perthshire
83	Creag nan Uamh Cave, Inchnadamph, Sutherland
84	Keshcorran Caves, Ballymote, Co. Sligo, Republic of Ireland
85	Edenvale Caves, nr Ennis, Co. Clare
86	Red Cellar Cave, nr Lough Gur, Co. Limerick
87	Castlepook Cave, Doneraile, Co. Cork
88	Castletownroche Cave, Connaberry, Co. Cork
89	Kilgreany Cave, Cappagh, Co. Waterford
90	Ballynamintra Cave, Whitechurch, Co. Waterford
91	Nornour, Isles of Scilly

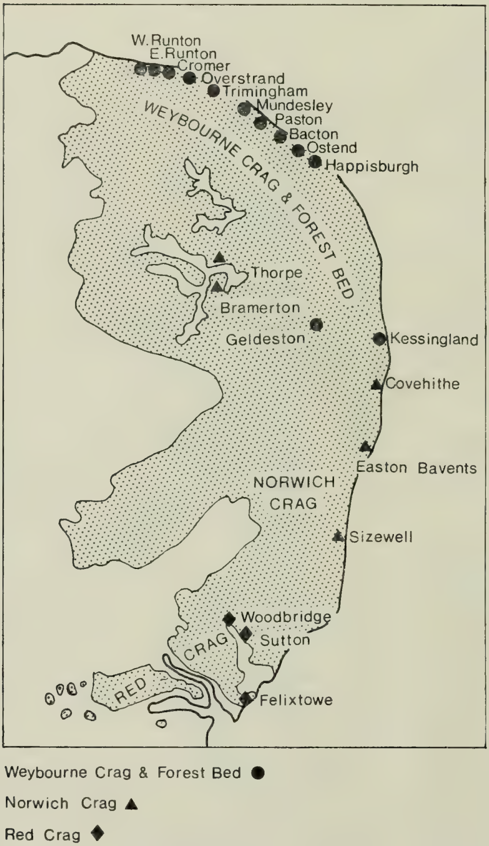

W. Runton
E. Runton
Cromer
Overstrand
Trimingham
Mundesley
Paston
Bacton
Ostend
Happisburgh
WEYBOURNE CRAG & FOREST BED
Thorpe
Bramerton
Geldeston
Kessingland
Covehithe
Easton Bavents
NORWICH CRAG
Sizewell
Woodbridge
Sutton
RED CRAG
Felixtowe
Weybourne Crag & Forest Bed ●
Norwich Crag ▲
Red Crag ◆

Fig. 2. Location map of Crag and Forest Bed rodent localities in East Anglia.

(iii) Cromer Forest Bed Series. This differs from the earlier Crag deposits in being predominantly estuarine and freshwater, with some beach deposits. Coastal exposures occur at many localities along the Norfolk coast, though these are unfortunately becoming increasingly obscured by sea defence work. Abundant remains of mammals (including rodents) and of plants occur in the Forest Bed. The most important rodent localities are West and East Runton (65, 64), with fewer remains from Ostend (57), Cromer (63), Overstrand (62), Mundesley (60), Paston (59), Bacton (58) and Kessingland (52).

It has long been recognized that all the Forest Bed deposits are not contemporaneous but that they accumulated over a considerable period of time, during which there occurred changes of climate and fauna. West & Wilson (1966), basing their conclusions on a study of plant remains, identified four climatic stages within the Forest Bed Series of deposits. In descending order these are :

Early Anglian	(cold, followed by glacial conditions during the later Anglian)
Cromerian *sensu stricto*	(warm)
Beestonian	(cold)
Pastonian	(warm)

Rodent remains are known from all horizons except the Beestonian. The Ostend Forest Bed presents a problem which is further discussed on pp. 48, 122.

(a) *Pastonian of East Runton and Happisburgh.* Only the earliest part of the Forest Bed sequence is represented at East Runton (64) ; deposits of Cromerian age, *sensu stricto*, apparently being absent. Azzaroli (1953) observed that the large mammals from this locality are Villafranchian species and that mammals present in the later part of the Forest Bed are absent. West (personal communication, 1972) considers, from palaeobotanical studies, that no Cromerian deposits, *sensu stricto*, have yet been proved on the foreshore at East Runton. He found, in descending order, the following sequence :

c. Clay Conglomerate, being reworked estuarine sediment, probably of Pastonian age, redeposited during late Pastonian or Beestonian times.
b. Shelly Crag, of Pastonian age, regarded by Hinton (1926b : 365) as Weybourne Crag.
a. Flint Bed, relating to a pre-Pastonian land surface.

Unfortunately the East Runton section has not been seen really well for many years and all the rodent remains available for the present study are from old collections. Three species of *Mimomys* are recorded ; these are *M. newtoni*, *M. pliocaenicus* and *M. savini*. The occurrence, together in the Shelly Crag, of the last two species, which represent successive stages in the development of the same phyletic line of voles, suggests the natural or accidental mixing of elements from different layers. *M. pliocaenicus* and *M. newtoni* are represented in both the Shelly Crag and among the 'clay pebbles' of East Runton, the holotype of *M. newtoni* being from the former horizon.

The precise stratigraphic range of these three species is far from clear. *M. savini* (represented by a few specimens from the Shelly Crag) is very abundant in the later, Cromerian *sensu stricto*, deposits of West Runton. The occurrence of remains of *M. pliocaenicus* and *M. newtoni* (known also from the earlier Norwich Crag) in the 'clay pebbles' could mean that these rodents persisted into Pastonian times. Such an interpretation would not be out of harmony with the 'Villafranchian' megafauna of this locality. The rolled condition of some of the remains could alternatively indicate their derivation from an earlier deposit.

Trogontherium boisvilletti and *Castor fiber* have also been found at East Runton.

A second Forest Bed locality, where the deposits are apparently of Pastonian age only, is Happisburgh (56). Remains of *Castor fiber* and also fir cones bearing marks which appear to indicate gnawing by squirrels (Newton 1882a) have been found there.

(b) *Beestonian.* No rodent remains are known from Beestonian deposits.

(c) *Cromerian* sensu stricto. The Upper Freshwater Bed of West Runton (65), defined by West (1961) as the type deposit of the Cromerian interglacial, contains abundant rodent remains. The following species are represented: *Apodemus sylvaticus, Trogontherium boisvilletti, Castor fiber, Cricetus cricetus, Mimomys savini, Clethrionomys glareolus, Pitymys arvaloides, P. gregaloides, Microtus arvalinus, M. nivaloides* and *M. ratticepoides. Muscardinus* recorded by Hinton (in Barrett-Hamilton & Hinton 1910–21, **2**: 351) from the 'Forest Bed' can possibly be added to the above list.

The rodent fauna with at least 11 species is unusually rich. It is predominantly of forest and meadow type, testifying to a mild climate; no arctic elements are present. The presence of *Cricetus* in this fauna is difficult to explain.

Sciurus whitei is represented from the marine 'Monkey Gravel' at West Runton, which overlies the Upper Freshwater Bed.

(d) *Anglian.* Newton (1882b) described some isolated worn teeth of *Spermophilus*, found in association with remains of arctic plants, in the Arctic Freshwater Bed near Mundesley (60). This deposit, which is immediately overlain by glacial till, has been interpreted as an indication of oncoming cold conditions in early Anglian times.

The rodent fauna of the Forest Bed deposits at Ostend (57) near Bacton presents a stratigraphic problem, since it cannot be accurately related to the above sequence. The remains include *Arvicola bactonensis* and *A. greeni* (Hinton 1926b: 386, 389), now both regarded as synonyms of *A. cantiana*, which led Hinton to conclude (p. 391) that the Ostend deposit is later than the Upper Freshwater Bed of West Runton. The specimens were collected over a century ago by the Rev. C. Green and unfortunately lack reliable stratigraphic information.

B. Terrace and Solifluxion deposits of the Rivers Thames and Lea

The richest series of rodent-bearing deposits related to a British river system is that of the River Thames and River Lea. The deposits of these rivers have been extensively worked commercially for gravel and brickearth and there have been many deep excavations for building foundations in the London area, leading to frequent discoveries of rodent remains (Fig. 3).

Three main series of deposits occur in association with these rivers, the exact relationship between which is often difficult to determine. Firstly, there are the terrace deposits of their upper courses, including Marlow and Isleworth in the Upper Thames, and Water Hall Farm Pit, Nazeing, Ponders End, Edmonton and Hackney on the River Lea. Deposits of both interglacial and glacial age occur here, those representing glacial stages merging with buried channels in the Lower Thames Valley province, where they are inaccessible for study in consequence of later rise of sea level.

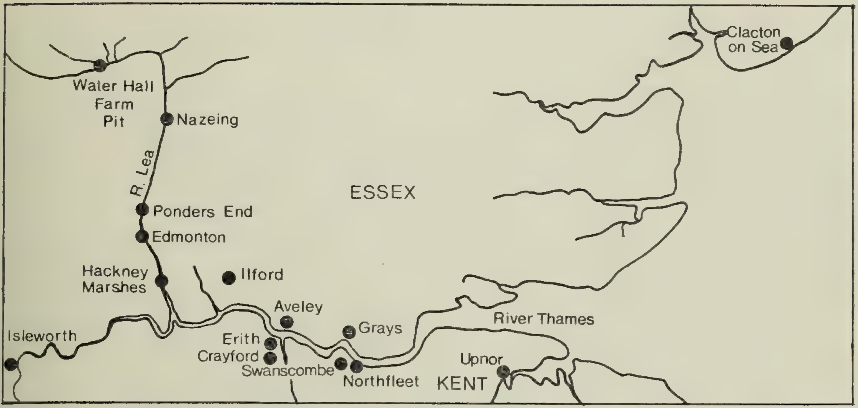


FIG. 3. Location map of rodent localities in the Thames estuary and the Lea valley.

Secondly, there are terraces of the Lower Thames, including Swanscombe, Clacton, Ilford, Aveley and Grays, Crayford and Erith. Hinton (1926b : 126–131) classified these as the High Terrace of the Thames (Swanscombe), the Early Middle Terrace (Grays Thurrock), and the Late Middle Terrace (Crayford and Erith). Whereas each terrace of the upper part of the river is of approximately constant height above the present-day bed of the river and thus becomes progressively lower as it is followed downstream, these terraces of the Lower Thames (which are related to former high sea levels) have approximately horizontal aggradation surfaces and they do not extend further upstream than the head of the contemporary tidal limit of the river. All are of interglacial or interstadial age and they can be correlated with raised beaches of similar heights along the open coastline. The cold stages which occurred between the accumulation of these terraces of the Lower Thames are represented by deposits submerged in the buried channels of the present-day river, previously mentioned.

Thirdly there are solifluxion and hillwash deposits, the heights of which are unrelated to the terrace system, with the deposits of which they are often interbedded. Northfleet is the only rodent locality, probably of this category, known to the writers.

It follows that, in an area as complicated as the valleys of the Rivers Thames and Lea, the exact relationship between the various rodent-bearing deposits is difficult to interpret. The literature on this subject, which goes back for nearly a century and a half, is voluminous. The general sequence was discussed by King & Oakley (1936) and in a number of important papers by Zeuner (e.g. 1954), who produced a schematic section from the Ebbsfleet Valley to Swanscombe, Kent, showing his interpretation of the relationship between the various deposits there. He interpreted the solifluxion and loess deposits with Levallois industries of Baker's Hole and Ebbsfleet as earlier than deposits of both Main Monastirian and Late Monastirian age, which he regarded as Last Interglacial, although only the Late Monastirian is accepted as Last Interglacial by Evans (p. 40).

During recent years J. N. Carreck has made a detailed further study of many of the mammalian localities in the Thames estuary, especially those in Kent, together with related museum collections and previous literature. On a basis of all lines of evidence he relates (*in litt.*) the deposits of some of the more important localities, here given in ascending stratigraphic order, as follows :

1. Interglacial deposits of Swanscombe, with Clactonian and Acheulean industries.
2. Interglacial deposits of Grays Thurrock and Little Thurrock (including the Orsett Road brickearths, but not those of West Thurrock, which are slightly later), Ilford and Aveley. The Ilford mammoth is a transitional form between *Mammuthus trogontherii* and *M. primigenius*. The Ilford fauna does not include any cold elements.
3. Deposits of the Baker's Hole cold stage at Ebbsfleet/Northfleet. The first true mammoth, *M. primigenius*, intermediate in form between the mammoths of Ilford and Crayford, appears at this locality in non-estuarine deposits overlying coombe rock (solifluxion) deposits. There are several associated Levallois industries.
4. Interglacial deposits of Crayford and Erith. Carreck found that the mammoth from the Lower Crayford Brickearth is more advanced than that from stage 3, though not so advanced as Last Glaciation mammoths from such localities as Ponders End, in the Lea valley, north London. He suggested that a layer of shattered chalk at the base of the Crayford sequence may be equivalent to the Baker's Hole cold stage and that the Crayford Gravel and Lower Brickearth, which are interglacial, follow immediately in time. The Crayford fauna suggests more open grassland conditions than indicated at Ilford or Grays, and there is a Levallois industry more advanced than that at Baker's Hole.
5. Other interglacial deposits, with hippopotamus, suggest that there may have been a further amelioration of climate. Carreck considers that the hippopotamus may have survived to a very late stage during the Last Interglacial. The Last Glaciation was characterized by a more advanced mammoth than that from Crayford.

Carreck pointed out that most of the Grays mammals were collected over a century ago, possibly from more than one terrace, which makes the study of this locality difficult ; he drew attention to the hazards of confusing the Baker's Hole cold stage, which he regarded as occurring within the Ipswichian Interglacial, with the Wolstonian/Saale Glaciation.

Carreck's chronological conclusions are of very far-reaching importance, with two points of special interest. Hinton's supposition that the Crayford deposits are later than those at Grays receives further support, but unlike the Geological Society (Mitchell *et al.* 1973), which regards the Northfleet coombe rock as Wolstonian and earlier than Ilford (which is regarded as Ipswichian), Carreck regards the Ilford deposits as being earlier than those of Northfleet.

Let us now consider in more detail the various deposits in the valley of the Thames and its tributaries where remains of fossil rodents have been found.

(i) LOWER THAMES.

(a) *High Terrace of Swanscombe.* One of the most important British rodent localities is the world-famous Swanscombe skull site (see Ovey (1964) for a fuller account). A series of estuarine deposits is aggraded to a height of approximately 31·5 m (103 ft) O.D. and is believed to have accumulated when the sea level rose to this height. Solifluxion deposits bring this figure to a total of 35·5 m (113 ft). Rodent remains have been found in two gravel pits, separated by a distance of about a third of a kilometre and now both disused. These are Barnfield Pit, where skull fragments of Acheulean Man were found, and Dierden's Pit, Ingress Vale. The following sequence of deposits has been described from Barnfield Pit :

6. The Upper Gravel. This is regarded as a solifluxion deposit, later than the terrace proper. No mammalian remains have been found in it.
5. The Upper Loam, with an Acheulean industry but no mammalian remains.
4. The Upper Middle Gravel, occupying a channel in the underlying deposits and containing an Acheulean industry. The top of this stratum, which is at about 31·5 m (103 ft) O.D., is regarded as the true surface of the terrace deposits proper. This deposit contains the '*Homo* layer' in which the human remains were found.
3. The Lower Middle Gravel, with an Acheulean industry.
2. The Lower Loam, with an *in situ* Clactonian activity horizon at its base and a knapping floor higher up. A zone of subaerial weathering, with many well-preserved animal footprints, is present on the surface of this deposit.
1. The Lower Gravel, with an early Clactonian industry, resting on a bench of underlying rock at 21–27 m (70–90 ft).

The deposits contain a rich molluscan fauna which has recently been re-examined by Kerney (1971). He concluded that the Lower Gravel, Lower Loam and the very base of the Lower Middle Gravel accumulated under temperate conditions, after which the climate became cooler.

Rodent remains have been found in the Lower Gravel (Carreck 1959), in the Lower Loam (remains recently excavated by Waechter), and in a silt bed in the Upper Middle Gravel at a level slightly higher than the '*Homo* layer' (Schreuder 1950). A few rodent remains have also been found at Ingress Vale. The distribution of rodent species at these two localities is shown in Table 3.

The exact relationship between the deposits of Barnfield Pit and Ingress Vale is uncertain. *Arvicola cantiana* occurs at both the latter site and in the Lower Loam of Barnfield Pit, suggesting a possible correlation of the two. Kerney (1971 and personal communication) found at Ingress Vale a temperate molluscan fauna associated with an industry which is culturally more advanced than that in the Lower Gravel and Lower Loam, suggesting to him a possible equivalence to the base of the Lower Middle Gravel.

The Swanscombe rodent remains are insufficiently abundant to permit reconstruction of any environmental and climatic changes, but the species of voles found in the

TABLE 3

Distribution of rodent species at Barnfield Pit and Ingress Vale, Swanscombe, Kent

	Barnfield Pit				
	Lower Gravel	Lower Loam	Lower Middle Gravel	Upper Middle Gravel	Ingress Vale
Trogontherium boisvilletti					×
Castor fiber		×			
*Apodemus sylvaticus**					×
Clethrionomys glareolus				×	
Arvicola cantiana		×			×
Lemmus sp.				×	
Microtus arvalinus		×		×	
M. ratticepoides		×		×	
Microtus sp. (*arvalis-agrestis* group)				×	
Pitymys arvaloides	×	×			

* Cited in earlier papers as *A. whitei*.

Lower Loam suggest that during the deposition of this layer a meadow environment may have prevailed. There are no arctic and no forest species, but such negative evidence is not decisive.

Although the Swanscombe deposits are generally regarded as being of Hoxnian Interglacial age, there is increasing evidence that a substantial interval may have elapsed between the deposition of the Lower Gravels/Lower Loam complex and of the overlying Middle Gravels. In general the rodent fauna of the lower unit quite closely resembles that of the Upper Freshwater Bed of West Runton. *Pitymys arvaloides*, *Microtus arvalinus* and *M. ratticepoides* occur in both the Upper Freshwater Bed at West Runton and in the Lower Loam at Barnfield Pit. The two abovementioned species of *Microtus* persist into the Upper Middle Gravel. *Mimomys savini*, characteristic of Cromerian assemblages *sensu stricto*, is nevertheless absent from Swanscombe, where it is replaced by *Arvicola*, absent from the Upper Freshwater Bed. It is of interest that by Upper Middle Gravel times *Lemmus* had appeared and *A. cantiana* may have disappeared. At the present day *Lemmus* is a rodent of northern latitudes. Whereas we have no means of demonstrating that its habit is not a recent adaptation, the occurrence of this genus could be interpreted as further evidence of the cool conditions indicated by the mollusca.

Recently Mullender (in Wymer 1974) has examined pollen from the Lower Loam of Barnfield Pit and found a marked break in the profile with a great increase in pine and near disappearance of alder. He equated the lower part of the Lower Loam with the Hoxnian Late-temperate Zone II and the upper part with the Wolstonian. If this interpretation were to be accepted then the later deposits of Barnfield Pit could no longer be referred to the Hoxnian, which would lead us to fresh problems of nomenclature for this part of the sequence.

(b) *Clacton.* The exact age relationship between the deposits of Clacton and Swanscombe is not clear, though Clacton is generally regarded as a further Hoxnian locality intermediate in age between the Lower Loam and Middle Gravel of Barnfield Pit. The Clacton deposits, which lie at about sea level, are at a lower altitude than those at Swanscombe. West (1972) suggests that slight downwarping has occurred in the Clacton area, which may explain this difference. There is a Clactonian industry. Plant remains from Clacton, studied by Pike & Godwin (1952), suggest about one-third of an interglacial sequence, during which mixed deciduous forest of the warmth maximum was replaced by coniferous forest.

Only a few rodent remains have been found in the Clacton deposits. These are *Trogontherium* cf. *cuvieri* (= *T. boisvilletti*) and *Clethrionomys* sp. (Singer *et al.* 1973), *Castor* sp. and *Microtus* of the *agrestis* group (Hinton 1923b), and *Arvicola* cf. *praeceptor* (= *A. cantiana*) (Warren 1955, quoting Hinton).

(c) *Early Middle Terrace at Aveley, Grays Thurrock and Ilford.* Hinton (1926b : 129) defined Grays Thurrock (33) as the type locality of this terrace of the Thames, with which the present writers also include Ilford (35) and Aveley (34). Table 4 lists those rodent species whose remains have been found at these localities.

The age of the deposits at these localities has been the subject of much discussion which is yet to be concluded. Hinton (1926b : 129–131) considered that the species of *Arvicola* from Grays (*A. praeceptor*, = *A. cantiana*) was not closely related to modern species of that genus. He considered that the latest Forest Bed deposits (presumably Ostend), the High Terrace of the Thames and the Early Middle Terrace were close in time. Zeuner (1945) considered Grays to be Hoxnian.

Hoxnian terrace deposits do indeed occur in the Grays area, though remains of fossil mammals do not seem to have been found in them. Wymer (1957) records terrace deposits of Hoxnian age with Clactonian implements resting on a bench at 15 m (49 ft) O.D., but points out that the Grays brickearth is later than this deposit. Most of the Grays rodent remains were found in the brickearth in a small pit near Orsett Road (Hinton 1901), about 650 m (700 yds) west of Wymer's site.

West (1969) studied plant remains from the three sites mentioned above and concluded that Aveley and Ilford are of Ipswichian age, and that Grays is interglacial, probably also Ipswichian. He pointed out that there was at this time apparently an important aggradation phase which resulted in the spreading of alluvium up to levels of between 12 and 15 m (40–50 ft) O.D.

The age of the Grays–Ilford–Aveley deposits will be further discussed below. From the evidence of the *Arvicola* remains, Grays Thurrock would appear to be relatively early.

TABLE 4

Distribution of rodent species at Grays Thurrock, Aveley and Ilford, Essex

	Grays Thurrock	Aveley	Ilford
Castor fiber	×		×
Apodemus sylvaticus	×		
Clethrionomys glareolus	×	×	
Arvicola cantiana	×	×	×
Microtus agrestis	×	*Microtus* sp.	×

(d) *Late Middle Terrace at Crayford and Erith.* A rich rodent fauna has been collected from the Thames terrace deposits of Crayford and nearby Erith ; it has been described by Kennard (1944). Owing to the lenticular character of the deposits at these localities there is little constancy in the details of the succession. Three broad divisions can, however, be identified. In descending order there are :

3. The Upper Brickearth, apparently not fluviatile but the result of sludging.
2. The Lower Brickearth and *Corbicula* Bed, up to 9 m (30 ft) O.D., laid down in a sluggish stream and in more strongly running water respectively. Levallois artefacts have been found in this deposit. Most of the rodent remains are from the *Corbicula* Bed.
1. The Lower Gravel, deposited by a fast-flowing river. The top was a land surface occupied by Levallois man, who left many artefacts.

Most of the rodent remains have been found in the *Corbicula* Bed, which is a sandy development of the Lower Brickearth. The following species are represented : *Spermophilus primigenius, Microtus oeconomus, M. nivalis, M. agrestis, Arvicola* sp., *Lemmus lemmus* and *Dicrostonyx torquatus.*

The age of the Crayford deposits is a topic requiring extensive further study. Hinton (1926b : 131) considered Crayford to be later than Grays, with a major intervening change of fauna. This view is also supported by Carreck (*in litt.*). At the present time Crayford is widely considered to be of Ipswichian age and both the freshwater and land mollusca found in the *Corbicula* Bed suggest conditions warmer than at the present time. The associated rodent fauna, however, is a typical assemblage of the 'penultimate' Glaciation. *Spermophilus primigenius* is unknown from the sediments of the Last Glaciation in Europe and, although *Microtus nivalis* was present during the Last Glaciation in many parts of Europe, and still survives in the mountains of central and south Europe, there is no evidence that it survived into the Last Glaciation in Britain.

It has been suggested that the lemmings burrowed into the *Corbicula* Bed from a later land surface, or alternatively that the remains were derived from an earlier deposit. Field evidence, however, suggests that the rodent remains are contemporary with the *Corbicula* Bed.

A total absence of forest species of land mollusca indicates that the country was open grassland. Living species of *Spermophilus* are also predominantly grassland animals. This could be interpreted as the beginning or end of an interglacial stage, though it is pointed out by Turner (in prep.) that riverside trampling by large herbivores can also give rise to clearances in otherwise wooded areas.

The Crayford deposits apparently date from some time during Wolstonian–Ipswichian times. Their precise stratigraphic position will be further discussed below and in Section IV (pp. 125–126).

(e) *Floodplain Terrace complex.* A series of lower terraces of Last Interglacial and Last Glaciation age in the Thames estuary have produced an abundance of remains of large mammals but, with one exception (*Castor* from the Upper Floodplain Terrace of the River Medway, a river flowing into the Thames estuary, at Upnor, Kent), no rodent remains are known from them.

(f) *The Middle Terrace/Floodplain Terrace problem.* Although no stratigraphically significant rodent remains have been found in the Floodplain Terrace complex of the Thames estuary, and although Hinton did not mention this terrace in his monograph (his 'Third Terrace of the Thames' is actually a terrace of the upper part of the River Lea), abundant rodent remains which are probably of Upper Floodplain Terrace age have nevertheless been found in many British cave deposits. The present section would be incomplete without some discussion of the status of this terrace.

It has already been pointed out that various workers have presented evidence that the period of time regarded by the Geological Society (Mitchell *et al.* 1973) as Hoxnian–Wolstonian–Ipswichian was, in fact, more complicated than this sequence suggests. Zeuner (1945) described evidence for a minor cool phase dividing what he regarded as the Last (Ipswichian) Interglacial into an earlier and a later part. He considered that there were two stages of high sea level during the Last Interglacial, the Main Monastirian or 18 m and subsequent Late Monastirian or 8 m shorelines, interrupted by an intra-Monastirian fall of sea level. These stages were accepted by Evans (1971 ; see pp. 40–42), though he argued that the earlier of these two stages should not be called Last Interglacial and observed that some confusion seemed to have arisen in archaeological circles where 'Last Interglacial' had been used for both.

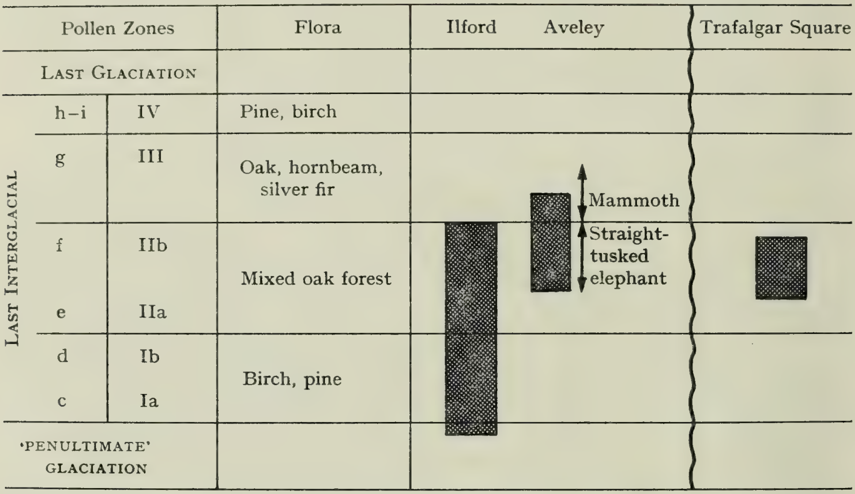
Zeuner correlated the so-called Taplow Terrace of the Thames estuary (our Middle Terrace complex belongs here ; the term 'Taplow' is best abandoned in the estuary since Taplow is in the upper part of the Thames and the terrace there is not estuarine) with the Main Monastirian sea level and the Upper Floodplain Terrace with that of the Late Monastirian. Both these supposed terraces are highly fossiliferous, with apparently different mammalian megafaunas.

When Zeuner described his interpretation of the Last Interglacial terrace sequence of the Thames estuary very little palaeobotanical evidence was available to him. During recent years, however, fossil plant remains have been found at a number of Last Interglacial localities there, the most important being Trafalgar Square (Franks 1960), Seven Kings Station, Ilford (West *et al.* 1964) and Aveley (West 1969), and here problems have arisen. The plant remains from these localities were assigned to the pollen zones shown in Table 5.

To those who had been studying the terraces and mammalian faunas of the Thames estuary, these results were surprising. Whereas Ilford and Aveley had appeared to be part of the Middle Terrace of the Thames and Trafalgar Square part of a lower terrace, the Upper Floodplain Terrace (i.e. Zeuner's two terraces of the Last Interglacial, representing two distinct periods of time), only one climatic fluctuation, with the climatic optimum of Zone IIb represented at all three sites, could be recognized from the pollen evidence. Was Zeuner wrong in separating the two stages of his supposed Last Interglacial, the Middle and 'Upper Floodplain' Terraces of the Thames estuary really being only one terrace, or are the floral remains from two separate climatic events so similar that these terraces cannot be distinguished on palaeobotanical evidence? Mammalian and morphological evidence suggests that, in agreement with the views of Zeuner and Evans, the latter

TABLE 5

Pollen zonation of some 'Ipswichian' interglacial sites in the Thames estuary



	Pollen Zones		Flora	Ilford	Aveley	Trafalgar Square
LAST GLACIATION						
LAST INTERGLACIAL	h–i	IV	Pine, birch			
	g	III	Oak, hornbeam, silver fir		▨	
	f	IIb	Mixed oak forest	▨	▨	▨
	e	IIa		▨	▨	▨
	d	Ib	Birch, pine	▨		
	c	Ia		▨		
'PENULTIMATE' GLACIATION						

Mammoth
Straight-tusked elephant

N.B. The Trafalgar Square deposits are of Zone IIb age, and should be shown somewhat higher than indicated.

alternative is the more likely even though palaeobotanical evidence supports only a single terrace (Fig. 4).

Even the chronological interpretation of the Ilford sequence is not without problems. West *et al.* (1964) referred the gravel under the Ipswichian brickearth and plant deposit at Seven Kings Station to the Gipping cold stage, but Carreck (*in litt.*) has pointed out that there is considerable lateral variation of the Ilford deposits with interglacial species of mollusca and mammals frequently present in the gravels and sands.

Let us now consider the large mammals of these Thames sites in some detail. At Trafalgar Square (supposedly Upper Floodplain Terrace) Zone IIb contains remains of hippopotamus, straight-tusked elephant, a rhinoceros which is probably *Dicerorhinus hemitoechus*, fallow deer, red deer, giant ox, bison, lion and other animals. No mammoth or horse remains were found. This is a faunal assemblage which occurs commonly in British cave deposits with localities as widely spread as Joint Mitnor Cave, Devon, and Kirkdale Cave, Yorkshire (Sutcliffe 1960).

The Ilford–Aveley fauna appears to be entirely different. At Ilford most of the elephant remains are of an early form of mammoth with affinities to the Middle Pleistocene *Mammuthus trogontherii*, though straight-tusked elephant is also represented. Two species of rhinoceros are present, *D. hemitoechus* and *D. kirchbergensis*. This last species is also common in the preceding Hoxnian Interglacial. There is an abundance of horse ; both hippopotamus and fallow deer are absent.

At Aveley straight-tusked elephant in Zone IIb is replaced by mammoth in Zone III. Comparison of rodent species unfortunately cannot be made, since no diagnostic remains have been found in the Upper Floodplain Terrace. *Arvicola cantiana* is present in the Middle Terrace at Aveley, Ilford and Grays Thurrock.

The megafaunas of Aveley and Ilford on the one hand, and of Trafalgar Square on the other, are so different that it is difficult to believe that they are contemporary, though consideration must be given to the possibility of their representing different stages within a single climatic fluctuation.

The evidence does not seem to support the latter alternative. The hippopotamus level at Trafalgar Square is Zone IIb. A vast amount of Zone IIb clay was excavated for cement-making at Aveley but no hippopotamus remains were found. The Ilford plant remains cover Zones IA–IIb but there were no hippopotamus remains there ; two specimens formerly attributed to this animal have since been shown to have been incorrectly identified.

It has been pointed out, in support of there having been only one temperate stage, that most of the Ilford mammal remains were recovered over a century ago, during excavations for brickearth which were relatively shallow and did not extend into

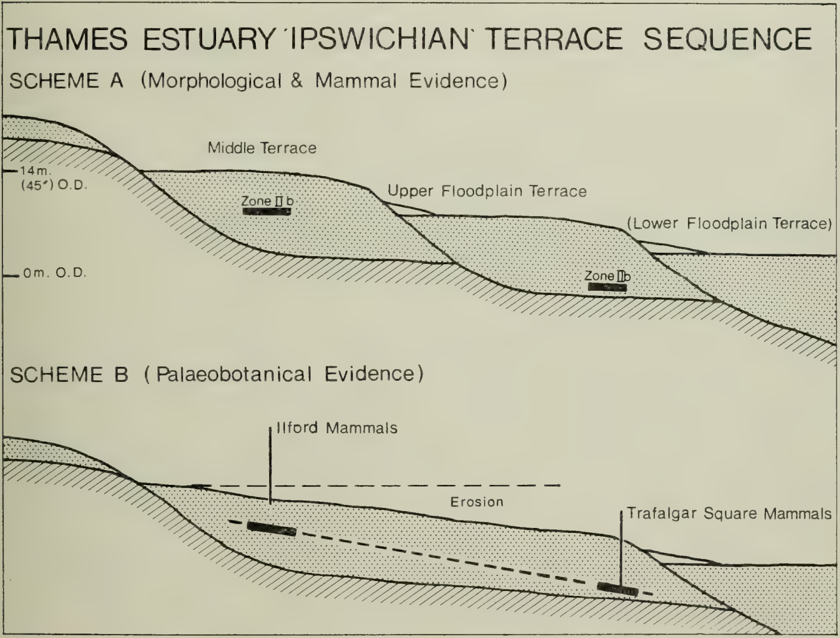

THAMES ESTUARY 'IPSWICHIAN' TERRACE SEQUENCE
SCHEME A (Morphological & Mammal Evidence)
Middle Terrace
14m. (45') O.D.
Zone IIb
Upper Floodplain Terrace
(Lower Floodplain Terrace)
0m. O.D.
Zone IIb
SCHEME B (Palaeobotanical Evidence)
Ilford Mammals
Erosion
Trafalgar Square Mammals

FIG. 4. Schematic section of Thames estuary Ipswichian terraces, showing alternative interpretations of the stratigraphic succession. Reproduced from Sutcliffe & Bowen (1973 : 18).

underlying gravel deposits, which were of no commercial value. The organic deposit described by West *et al.* (1964) at Seven Kings Station underlay the brickearth, so it is possible that the Ilford mammalian fauna is later than Zone IIb (perhaps Zone III), that is the Trafalgar Square fauna might have been found in the basal part of the Ilford terrace had excavations been carried deeper. According to this theory Trafalgar Square represents an earlier stage than Ilford ; according to the twin terrace theory it is later. The former interpretation presents several difficulties. In spite of extensive commercial excavation of sand and clay in the London area, no such relationship has ever been observed ; the Upper Floodplain Terrace does appear to be a good morphological feature ; the Ilford mammoth is relatively primitive ; the Ilford fauna has never been recognized in any British cave, with the possible exception of Hutton Cave, whereas the Trafalgar Square fauna with hippopotamus occurs frequently, suggesting that such deposits have been subject to less denudation and are more recent.

In the absence of diagnostic rodent species in the Upper Floodplain Terrace of the Thames the above problem cannot at present be resolved from studies in the Thames area. It will be further critically examined below, in the section on hippopotamus faunas in caves and in Section IV.

(ii) UPPER THAMES.

(a) *Isleworth.* Remains of *Microtus oeconomus* and *M. gregalis* were found at Willment's Gravel Pit, Isleworth, in a deposit where they were associated with remains of temperate mollusca and insects (Coope, 1975) and with plant remains dated by ^{14}C to 43 140 + 1520 or − 1280 years B.P. (Birmingham 319). This deposit was overlain by sands and gravels containing remains of reindeer and cut by many fossil ice wedges. A description of the site, by J. Simons, is in preparation. The sequence is interpreted as indicating deteriorating climatic conditions after an interstadial during the Last Glaciation. It is probably the earliest occurrence of *M. gregalis* in Britain ; this species appears to be restricted there to the Last Glaciation and to have disappeared before the end of that stage.

(b) *Marlow.* A small sample of brickearth, found in the Treacher collection at the British Museum (Natural History) and labelled as coming from a brickearth pit 1 mile north-east of Marlow, was found to be rich in rodent remains, predominantly dissociated teeth. They were examined by Dr G. B. Corbet who found that most of them were apparently of *Microtus arvalis.* There was also one first lower molar of *M. oeconomus.* The lack of any second upper molars of *M. agrestis* and the occurrence of only one first lower molar of *M. oeconomus* among the many first lower molars (which teeth distinguish these last two closely related species from *M. arvalis*) suggest *M. arvalis* was the principal species present.

The age of the Marlow rodents is uncertain, but it is likely to be Last Glaciation. Neither *M. arvalis* nor *M. oeconomus* survives on the mainland of Britain at the present day.

(iii) RIVER LEA.

(a) *Water Hall Farm Gravel Pit.* An important sequence of Pleistocene deposits occurs at Water Hall Farm, Hertfordshire. Here the valley of the River Lea has cut through earlier glacial deposits which still cap the hills on either side. In the valley bottom the River Lea is flanked on one bank by its present-day floodplain, on the other by a slightly higher terrace in which have been found abundant remains of interglacial mammals, including *Hippopotamus* and *Palaeoloxodon antiquus*. Remains of *Mammuthus* have also been found. At the base of the sequence of deposits in this terrace there was formerly exposed a white marl with remains of amphibia and of the rodents *Microtus agrestis*, *M. oeconomus* and *M. nivalis*. Since most of the commercial excavation of the interglacial terrace, since concluded, was carried out by mechanical excavators, the exact stratigraphic relationship between the hippopotamus layer and the rodent layer remains unproved, but nearly the whole of the ossiferous gravel deposit for which the pit was worked overlay the rodent-bearing marl and there seems no doubt that the rodent remains antedate those of the hippopotamus. Unfortunately no rodent remains have been found in the upper deposits.

The sequence of events at this locality is provisionally determined as follows :

1. Boulder clay and glacial deposits. Not later than 'penultimate' glaciation.
2. Retreat of ice and valley deepening by River Lea.
3. Deposition of marl with remains of amphibia and rodents.
4. Deposition of interglacial deposits with *Hippopotamus* and *P. antiquus* overlying the rodent marl. Last Interglacial.
5. Further deepening of Lea Valley and formation of present floodplain. Last Glaciation to present day.

(b) *Nazeing, Ponders End, Edmonton and Hackney*. A complex series of deposits, mainly of late Last Glaciation and Holocene age, occupies the valley of the lower part of the River Lea. Rodent remains have been found at a number of localities there. The most important of these is at Nazeing, where a series of channel, lake and marsh deposits have been palaeobotanically dated as ranging from Late Glacial to post-Glacial vegetation Zone VII, providing the latest known survival dates in Britain for a number of rodent species (Hinton 1952). The late Pleistocene part of the sequence produced remains of *Microtus oeconomus*, *M. gregalis*, *Arvicola terrestris*, *Lemmus lemmus* and *Dicrostonyx torquatus*. Of these the last-mentioned species and *M. gregalis* were still present in Late Glacial pollen Zone III and *M. oeconomus* appears to have survived possibly until post-Glacial Zone V. *Arvicola terrestris* also persisted into the Flandrian and *Apodemus sylvaticus*, *Clethrionomys glareolus* and *M. agrestis* appear in Zones V–VI, by which time post-Glacial re-afforestation had reached an advanced stage.

Remains of *Dicrostonyx torquatus* have been found at three other late Pleistocene localities in the Lea Valley : Ponders End (Warren 1916), Angel Road, Edmonton (Hinton 1912) and at Hackney.

(iv) SOLIFLUXION AND MELT-WATER DEPOSITS.

(a) *Northfleet, Ebbsfleet and Baker's Hole*. Burchell (1935) recorded finding rodent remains associated with those of mammoth and rhinoceros in non-estuarine deposits filling a channel cut through a coombe rock (solifluxion) deposit at Baker's Hole, between Northfleet and Swanscombe, Kent. As previously mentioned (p. 50) Carreck (*in litt.*), from the study of the mammoth remains from this site, considered that the deposits, which indicate an ameliorating climate following the deposition of the coombe rock, are later than those of Ilford but earlier than Crayford. Stuart (*in litt.*), who has recently re-examined the Burchell specimens in the British Museum (Natural History) together with a few specimens collected more recently by Kerney and Sieveking, gives the following list of species : *Clethrionomys glareolus*, *Microtus arvalis/agrestis* and *Arvicola cantiana*. He found that in teeth of the last-mentioned species the enamel is clearly differentiated, as in *Mimomys*, with no *A. cantiana-terrestris* intermediate forms (see notes on *Arvicola*, pp. 99–102). This suggests a relatively early date for the Northfleet rodent remains, a conclusion in agreement with Carreck's observations on the mammoth remains. Burchell (1935) listed *Microtus arvalis* (here interpreted as *M. arvalis/agrestis* group), *M. nivalis* and *M. anglicus* (= *M. gregalis*) from his excavations, but the last two have not been confirmed by Stuart's re-examination of the available specimens.

C. Cave Deposits

Remains of Pleistocene rodents have been found in many caves in the British Isles. Most such deposits accumulated in consequence of animals accidentally falling down shafts or of their remains being carried into caves by birds of prey. Since, however, the entrance parts of caves are vulnerable to destruction by processes of denudation, many formerly-existing rodent deposits have since disappeared ; it is unusual to find any rodent remains in caves of earlier than Upper Pleistocene age. Kent's Cavern and a recently discovered fissure at Westbury-sub-Mendip, Somerset, are probably the only exceptions. A Lower Pleistocene cave deposit with megafauna has also been found at Dove Holes, Derbyshire (Crag age), but unfortunately no contemporary rodent remains have been recorded. In contrast, cave deposits with Last Glaciation and Holocene rodent remains are very numerous.

Few of these sites have produced stratified sequences of rodent faunas, either because the deposits accumulated during only a short period of time, because they had been disturbed before excavation, or because they were excavated before the importance of stratigraphy had become adequately appreciated.

The following are the most important rodent caves in the British Isles.

(i) WESTBURY FISSURE (13). The recently discovered fissure infilling at Westbury-sub-Mendip, described by Bishop (1974, 1975), is of special importance, since its rich mammalian fauna indicates a stage slightly later than the type Cromerian of West Runton, not otherwise well represented in the British Pleistocene. Bishop described, in descending order, the following sequence of deposits :

III. 'Rodent Earth' (layer 10, the upper part of the 'Calcareous Group', layers 2–9 below). A deposit with an abundance of remains of rodents and other small mammals, possibly an accumulation of pellets of birds of prey.

II. 'Calcareous Group' (layers 2–9, excluding the 'Rodent Earth'). Predominantly limestone breccias with abundant remains of bears. The cave was probably a bear den at this stage.

I. 'Siliceous Group' (layer 1). Water-laid deposits with some rolled bones and teeth.

TABLE 6

Stratigraphic distribution of rodent species in the Westbury Fissure (after Bishop 1974, with personally communicated additions)

	Bed number	*Castor fiber* Linn.	*Apodemus sylvaticus* Linn.	*Dicrostonyx* sp.	*Lemmus* sp.	*Clethrionomys glareolus* Schreber	*Pliomys episcopalis* Méhely	*Arvicola cantiana* Hinton	*Pitymys gregaloides* Hinton	*Microtus arvalinus* Hinton
III. 'Rodent Earth'	10		×	×	×	×	×	×	(common) ×	×
II. 'Calcareous Group' (excluding 'Rodent Earth')	2–9		×		×			×	×	×
I. 'Siliceous Group'	1	×								

The distribution of rodent species in the Westbury fissure is shown in Table 6.

The age of the deposit has been discussed in detail by Bishop (1974). From the 'Calcareous Group', excluding the 'Rodent Earth', he recorded a fauna including *Homotherium latidens, Felis gombaszoegensis, Ursus deningeri, Xenocyon lycaonoides, Canis lupus mosbachensis, Dicerorhinus etruscus* and *Equus mosbachensis.* Rodents from this level are *Apodemus sylvaticus, Lemmus* sp. (the earliest record of this genus in the British Pleistocene), *Arvicola cantiana, Pitymys gregaloides* and *Microtus arvalinus.* The same species are represented in greater abundance in the 'Rodent Earth', which Bishop regarded as the last stage of the 'Calcareous Group'. Remains of *Pliomys episcopalis* (the first record in the British Pleistocene), *Dicrostonyx* sp. (the earliest record in the British Pleistocene) and *Clethrionomys* were also found in the 'Rodent Earth'.

Bishop regarded the Westbury fauna as later than the type Cromerian of West Runton but not later than Elsterian. He drew attention to its similarity to that of the classic 'late Cromerian' sites of Europe (in particular Mauer, Hundsheim, Tarkö and Mosbach) and equated the Westbury 'Rodent Earth' with the *Arvicola* fauna group 1 of Koenigswald (1973) (see pp. 100–101). This stage was previously unrecognized in the British Pleistocene sequence.

(ii) KENT'S CAVERN. Unfortunately most of the rodent remains found in Kent's Cavern were excavated during the nineteenth century and only sparse stratigraphic information is associated with them. The following species have been found there (Hinton 1915, Kennard 1945–6, British Museum (Natural History) collection):

Castor fiber, Apodemus flavicollis, Clethrionomys glareolus, Arvicola terrestris, Dicrostonyx torquatus, Lemmus lemmus, Pitymys gregaloides, Microtus agrestis, M. oeconomus and *M. gregalis.* In addition, Campbell & Sampson (1971) recorded a specimen of *Arvicola greeni* (regarded here as a synonym of *A. cantiana*) among specimens collected from the cave by J. MacEnery between 1825 and 1829. This is a typically Last Glaciation–Holocene fauna, with the exception of *P. gregaloides*, not recorded elsewhere in Britain in deposits later than those of the Westbury Fissure, and *A. cantiana.* The occurrence of *P. gregaloides* and also sabre-toothed cat, *Homotherium*, in Kent's Cavern has been interpreted by both Hinton (1926b) and Campbell & Sampson (1971) as evidence of a Cromerian stratum somewhere in Kent's Cavern.

The sequence of deposits in the cave varies from one chamber to another (for details see Campbell & Sampson). The principal deposits, in descending order, are as follows :

5. Black Mould, with Mesolithic and later artefacts and fauna.
4. Granular Stalagmite, with Mesolithic and Neolithic artefacts and fauna.
3. Cave Earth, including a local area of hearths known as the Black Band. Middle to Upper Palaeolithic industries. Mammalian fauna including woolly mammoth, woolly rhinoceros and hyaena.
2. Crystalline Stalagmite.
1. Breccia, with many bear remains and with a Lower Palaeolithic industry.

The upper part of the above sequence is typically Last Glaciation (the Cave Earth) to Holocene. Most of the rodent remains probably come from the upper levels. *Pitymys gregaloides*, on the other hand, is a Middle Pleistocene species probably derived from the Breccia, the age of which is at present uncertain. *Homotherium, P. gregaloides* and *A. cantiana* are all recorded from the Westbury Fissure. At the present time it seems most likely that the earliest remains from Kent's Cavern are of Westbury Fissure age. There is no conclusive evidence of fauna as early as Cromerian *sensu stricto*. It may be inferred that the Crystalline Stalagmite represents a major break in sedimentation, possibly because the cave entrance had become sealed.

(iii) TORNEWTON CAVE (3). The most important sequence of stratified cave deposits with rodent remains known from the British Isles is that of Tornewton Cave, south Devon (Sutcliffe & Zeuner 1962, Kowalski 1967). Deposits in the shaft-like Main Chamber of this cave and of the talus deposits outside span a cold–interglacial–cold sequence which is unique in showing differences between the rodent faunas of the two cold stages concerned. The relationship between this sequence and that of the terraces of the River Thames will be considered in Section IV, pp. 124–127.

The principal deposits in the Main Chamber of Tornewton Cave (excluding some superficial deposits excavated during the nineteenth century and a series of stalagmite floors), in descending order, were found to be as follows :

5. 'Diluvium'. Most of this deposit was excavated during the nineteenth century. The remaining part contained a few remains of wolf, hyaena, bear, bovid and

reindeer. A Holocene molluscan fauna has been identified by M. P. Kerney from this horizon and it is probable that the mammalian remains are a mixture of derived Pleistocene and contemporary Holocene species.

4. The Reindeer Stratum. Most of this deposit was excavated from the Main Chamber of the cave during the nineteenth century. Abundant rodent remains, associated with remains of wolf, hyaena, horse, rhinoceros, reindeer, a bovid and a sparse Upper Palaeolithic industry were nevertheless recovered more recently from an extension of this stratum in the talus outside the cave. The stratum is of Last Glaciation age.
3. The Hyaena Stratum. A deposit with abundant remains of spotted hyaenas, which animals apparently occupied the cave as a lair, associated with occasional remains of hippopotamus, narrow-nosed rhinoceros, red and fallow deer, lion, wolf and bear. This is an interglacial assemblage, tentatively referred to the 'Ipswichian'.
2. The Bear Stratum. A deposit with abundant remains of brown bears, which animals used the cave as a lair at this stage.
1. The Glutton Stratum. The earliest fossiliferous deposit in the cave, with numerous remains of brown bears associated with occasional remains of glutton (wolverine) and reindeer. This deposit represents an earlier cold phase.

Table 7 shows the stratigraphic distribution of rodent remains in the Main Chamber and (Reindeer Stratum only) in the talus of Tornewton Cave. It will be seen from the table that, in the Glutton Stratum, *Microtus oeconomus* and *M. nivalis* make up the bulk of the rodent fauna. *Lagurus lagurus* (from the only British locality with this genus), *Allocricetus bursae* and *Cricetus cricetus* are typical species of the 'penultimate' glaciation. *Dicrostonyx torquatus* and *Lemmus lemmus*

TABLE 7

Number of rodent specimens from the main deposits of Tornewton Cave

	Glutton Stratum	Bear Stratum	Hyaena Stratum	Reindeer Stratum	'Diluvium'	Total
Apodemus sylvaticus	1	–	1	–	8	10
Cricetus cricetus	4	–	–	–	–	4
cf. *Allocricetus bursae*	4	–	–	–	–	4
Dicrostonyx torquatus	7	2	–	7	1	17
Lemmus lemmus	1	1	–	–	–	2
Clethrionomys glareolus	11	3	–	12	4	30
Arvicola sp.	36	1	2	14	2	55
Microtus agrestis	170	4	6	123	77	380
Microtus nivalis	298	4	–	–	–	302
Microtus oeconomus	1066	15	–	19	9	1109
Microtus gregalis	–	–	–	43	12	55
Lagurus lagurus	62	1	–	–	–	63
Total	1660	31	9	218	113	2031

The count is based on the number of determinable specimens, not individuals. The apparent greater abundance of remains in the Glutton Stratum is the result of more extensive sampling of this deposit. Remains from minor deposits not included above bring the total number of specimens determined to 2383.

are present but not abundant. *Microtus gregalis* is absent. Sylvan species are very rare, though a few remains of *Clethrionomys glareolus* occur with this predominantly meadow and steppe assemblage. A single tooth of *Apodemus sylvaticus* probably represents contamination of the deposit. The rodent fauna of the Glutton Stratum has affinities to that of Crayford, Kent, from which it was probably not greatly separated in time.

Only a few rodent remains were collected from the Bear Stratum. The fauna does not differ in composition from that of the underlying Glutton Stratum though, with the exception of one tooth of *Lagurus lagurus* and four of *Microtus nivalis*, the typical 'penultimate glaciation' elements are lacking. Their absence could be accidental, however, since they are also rare in the Glutton Stratum. The absence of lemmings could indicate a slight amelioration of climate.

Rodents are poorly represented in the Hyaena Stratum. *Apodemus sylvaticus*, represented by only one specimen, is a forest species. *Microtus agrestis* and *Arvicola* sp. are ecologically neutral.

The Reindeer Stratum has a predominantly cold fauna with the typically Last Glaciation *Microtus gregalis* and with *Dicrostonyx torquatus*.

The apparent mixture of arctic and sylvan species in the 'Diluvium' is in agreement with this deposit being of Holocene age, with derived Pleistocene remains. *Apodemus sylvaticus* reappears here. The climate was milder than before.

The sequence of rodent faunas described above is of great importance as it makes possible, for the first time, distinction between mammalian assemblages, indistinguishable on the basis of the larger mammals, of the two cold stages concerned. Arctic elements (for example, lemmings) appear twice in the sequence, but are lacking from the interglacial Hyaena Stratum. The lower cold stage is characterized by, among other rodents, *Cricetus cricetus*, cf. *Allocricetus bursae*, *Lagurus lagurus* and *Microtus nivalis*, all absent from the Reindeer Stratum, where they are replaced by large quantities of *M. gregalis* which, on the other hand, is absent from the Glutton Stratum.

Distinction is also possible between the teeth of *Arvicola* from the Glutton Stratum and those from the Reindeer Stratum. W. von Koenigswald (1973 and personal communication) has found that although the form from the latter deposit is *A. terrestris*, that from the Glutton Stratum is an intermediate form tending towards *Arvicola cantiana*, known from the Middle Pleistocene deposits of Swanscombe (see pp. 100–102).

In addition to the deposits of the Main Chamber of Tornewton Cave two important rodent deposits were found in positions where they could not be directly related to the main sequence. These are the Otter Stratum, in a small chamber adjoining the Main Chamber, and the Upper Rodent Stratum, on the rock platform outside the cave mouth.

The Otter Stratum was found to contain an abundance of remains of brown bears associated with some mammalian species unrecorded elsewhere in the Pleistocene of the British Isles, notably *Cyrnaonyx*, the clawless otter, and *Crocidura*, the white-toothed shrew (Rzebik 1968). It was composed of a mixture of broken stalagmite blocks, some containing faunal remains, in an earthy matrix, suggesting some disturbance of the deposit. The following rodent specimens were collected from it.

Cricetus cricetus	2 specimens
Lagurus lagurus	1 specimen
Dicrostonyx torquatus	1 specimen
Lemmus lemmus	1 specimen
Microtus nivalis	4 specimens
Microtus oeconomus	82 specimens
Apodemus sylvaticus	2 specimens
Clethrionomys glareolus	19 specimens
Microtus agrestis	5 specimens
Arvicola sp.	8 specimens

This fauna appears to be a mixture from two originally separate layers. Remains from a warm period, including *Microtus oeconomus,* predominate. They point to a last interglacial age. No Hoxnian elements are present. *Lagurus lagurus, Cricetus cricetus* and *Microtus nivalis,* on the other hand, are species of the 'penultimate' glaciation. In an attempt to separate the two faunal assemblages some of the stalagmite blocks were dissolved in acid. Only temperate species (*Microtus agrestis,* 1 determinable specimen ; *M. oeconomus,* 6 ; *Arvicola* sp., 1 ; *Clethrionomys glareolus,* 4 ; *Apodemus sylvaticus,* 1) were found in the stalagmite. The exact stratigraphic relationship between the Otter Stratum and the deposits of the Main Chamber of Tornewton Cave is unfortunately uncertain, since the overlying deposits were excavated during the nineteenth century and are no longer available for examination. The cave was apparently still inhabited as a lair by bears, making it probable that the deposit antedates the Hyaena Stratum. On the other hand, it seems to be later than the Glutton Stratum since Koenigswald has found that, whilst the *Arvicola* from both the Glutton Stratum and the Otter Stratum is an intermediate form between *A. cantiana* and *A. terrestris,* that from the Otter Stratum is slightly more advanced, though not so advanced as the form from the Reindeer Stratum, which is *A. terrestris.* The Otter Stratum fauna appears to be a unique assemblage, unknown from any other locality in the British Isles.

The deposit known as the Upper Rodent Stratum occupied a rift on the rock platform outside the main entrance to Tornewton Cave. It was only a short distance below the surface and is probably of modern date. The following species are represented : *Apodemus sylvaticus,* 58 specimens ; *Clethrionomys glareolus,* 14 ; *Microtus agrestis,* 86 ; *Arvicola terrestris,* 2 ; *Micromys minutus,* 1. All these species live near the cave at the present day, no extinct species are represented ; and *M. minutus* is a late arrival probably associated with neighbouring plough-land.

In conclusion the relative proportions of the various ecologic groups of rodents represented in Tornewton Cave are shown in Table 8.

(iv) OTHER CAVES WITH PRE-'IPSWICHIAN' DEPOSITS. In light of the faunal sequence demonstrated at Tornewton Cave, it would be surprising if other rodent faunas dating from the time interval between the Hoxnian and the warm stage represented by the Hyaena Stratum of Tornewton Cave were not to be found in caves from time to time. At present this period is one of some obscurity.

TABLE 8

The relative proportions of the various ecologic groups of rodents found in Tornewton Cave

Layer	Tundra and steppe	Boreal	Forest	Neutral
Upper Rodent Stratum	0	0	44·7	55·3
'Diluvium'	11·5	8·0	10·6	69·9
Reindeer Stratum	22·9	8·7	5·5	62·8
Hyaena Stratum	0	0	2·3	97·7
Bear Stratum	25·8	48·4	9·6	16·1
Glutton Stratum	22·7	64·2	0·7	12·4

Tundra and steppe elements include *Dicrostonyx torquatus, Lemmus lemmus, Microtus gregalis, M. nivalis, Lagurus lagurus, Cricetus cricetus* and *Allocricetus*. Boreal elements include *M. oeconomus*. At the present day this species lives mainly in the taiga belt but it also occurs, under milder climatic conditions, in marshland. The forest element is represented by *Apodemus sylvaticus* and *Clethrionomys glareolus*. *Arvicola* sp. and *M. agrestis* are 'neutral' in their ecologic requirements. *Micromys* has been omitted from the table since it was probably introduced by man.

Some isolated pre-'Ipswichian' rodent-bearing cave deposits have nevertheless apparently been found. Hinton (1926b) regarded the rodents of Clevedon Cave (14) and Banwell Cave (10), Somerset, as probably contemporary with those of Crayford which, we have observed, are similar to those of the Glutton Stratum of Tornewton Cave. The rich material from Clevedon Cave is of special interest, as it contains only two species of rodents, *Microtus nivalis* and *M. oeconomus*. Hinton (1907a) wrote : 'Dr H. C. Male very generously presented me with a small series of the numerous jaws of *Microtus* which he found in the Clevedon deposit.' In the material described by Hinton, which is still preserved in the British Museum (Natural History), there are exclusively remains of the species mentioned above. It is possible that Dr Male did not present Hinton with the material of the other rodents, but it does not seem possible that he retained jaws of *Microtus agrestis*, as they are difficult to distinguish from those of *M. nivalis* except by a specialist. It seems probable that the Clevedon Cave remains accumulated at a time when the rodent fauna was composed exclusively of *M. oeconomus* and *M. nivalis*.

Hinton's specimens from Banwell Cave have not been seen by the present writers. The only available specimens, representing *Arvicola* sp. and *Microtus* sp., are stratigraphically inconclusive.

The Gough's Cave (12) rodent fauna is composed of *Arvicola* sp., *Microtus agrestis*, *M. oeconomus* and *M. nivalis*. The last-mentioned species suggests an age equivalent to the Glutton Stratum at Tornewton Cave, though the occurrence of a late Upper Palaeolithic industry in the cave indicates a more recent date for most of the deposits.

The occurrence of *M. nivalis* among various rodent remains excavated by J. Simons from Cow Cave, Chudleigh, Devon (7), suggests that there may be a pre-'Ipswichian' deposit there.

Hutton Cave, Somerset (10), may provide a further example of a pre-'Ipswichian' rodent locality. One of the rodents found there, cf. *Allocricetus bursae*, is known elsewhere in the British Isles only from the Glutton Stratum of Tornewton Cave.

A primitive form of mammoth further supports a relatively early date for the fauna of this cave.

(v) 'IPSWICHIAN' CAVE DEPOSITS. Sites, in addition to Tornewton Cave, include the hippopotamus-bearing deposits of Joint Mitnor Cave, Devon (1), with *Arvicola cantiana-terrestris* transition form (determined by W. von Koenigswald) and *Microtus agrestis*; Minchin Hole, Glamorganshire (16), with the same species; the nearby Bacon Hole (16) recently excavated by C. Stringer (1975) with *Arvicola* sp., *M. agrestis*, *Clethrionomys glareolus* and *M. oeconomus*; and Alveston Fissure, Gloucestershire (15), with *M. agrestis* and *Clethrionomys* sp. Rodent remains from the interglacial site of Kirkdale Cave, Yorkshire (77), include *Arvicola* sp., *M. agrestis*, *Clethrionomys* sp., *Apodemus sylvaticus* and *Dicrostonyx torquatus*. This cave was excavated over a century ago. *Dicrostonyx* is out of place and suggests some mixing of material.

The rodent fauna of this stage is typically sparse, with *Arvicola cantiana-terrestris* transition form and *Microtus agrestis* the most common species.

(vi) CAVES WITH POST-IPSWICHIAN DEPOSITS. Cave deposits dating from the Last Glaciation and Holocene are far more numerous than earlier deposits, since there has been less time for them to be destroyed by denudation. Many examples are known. The distribution of rodent species at some of the more important cave sites believed to date from this period is shown in Table 10 (pp. 70–71; for references, see Section III).

The interpretation of these rodent faunas must unfortunately be undertaken with caution since many of the deposits in which they were found had been disturbed by burrowing animals; some important rodent caves were excavated during the nineteenth century, so that adequate stratigraphic information is lacking. A fairly consistent Pleistocene faunal assemblage is nevertheless apparent, with *Sciurus vulgaris*, *Muscardinus avellanarius*, *Apodemus flavicollis* and *Rattus rattus* probably not arriving until Holocene times. A series of excavations recently conducted by the Peakland Archaeological Society in Derbyshire and Staffordshire (Bramwell 1960, 1964, 1970; Pernetta 1966) is of special interest for the light thrown on the rodent faunas of the end of the Pleistocene and early Holocene. The two lemmings, *Lemmus* and *Dicrostonyx*, appear to have been common until the end of the Pleistocene after some of the large Pleistocene mammals, such as woolly rhinoceros and hyaena, had disappeared; *Microtus oeconomus* seems to have survived into post-Pleistocene times. The apparent absence of lemmings at Levaton Cave (2, a Pleistocene site with mammoth, woolly rhinoceros, red deer, reindeer and hyaena) suggests that, during part of the Last Glaciation (probably an interstadial), *Lemmus* and *Dicrostonyx* may have been absent from the fauna, at least in the south of England. The Ightham fissures, Kent (Abbot 1917; Newton 1894, 1899a, b), are further important cave sites with rodent remains of Last Glaciation age. All the fissures do not appear to be contemporary, however, and there may have been some mixing of Holocene material.

(vii) CAVES IN SCOTLAND. A series of small caves near Inchnadamph in Scotland (83) are of special interest as including the most northerly British fossil rodent locality. From one of them, Creag nan Uamh Cave, Newton (in Peach & Horne 1917) recorded *Dicrostonyx torquatus*, *Microtus agrestis* and *M. ratticeps* (= *M. oeconomus*). Remains of brown bear, reindeer and lynx were also found at the same site. The age of these remains is uncertain, but the caves are situated in wild mountainous country and the possibility that they are of relatively late age needs to be taken into consideration. Some bones of brown bear found in a nearby cave have recently been dated by ^{14}C as only about 2700 years old (Burleigh 1972).

(viii) CAVES IN IRELAND. Most rodent species living in Ireland today are probably post-Pleistocene arrivals. Only four possibly Pleistocene species need to be considered here. Their distribution at cave sites is shown in Table 9.

The exact stratigraphic position of these various remains is uncertain, although it seems unlikely that any of the Irish mammalian faunas are earlier than Last Glaciation. Mitchell (1969) considered that the mammals could not all be attributed to one phase, suggesting that, although the remains of giant deer and reindeer found beneath the peat bogs were known to be of Late Glacial age, the Castlepook Cave fauna dated from an (earlier) interstadial of the Last Glaciation. A recently obtained ^{14}C date for part of a mammoth bone from Castlepook Cave (33 500 ± 1200 years B.P., University of Dublin 122) confirms Mitchell's supposition.

Both *Lemmus* and *Dicrostonyx* are northern species which might be expected to have reached Ireland in advance of other rodent species. Associated species in

TABLE 9

Distribution of rodent species at Irish cave sites

						Edenvale caves, Co. Clare (85)				Keshcorran Caves, Co. Sligo (84)	
	Ballynamintra Cave, Co. Waterford (90)	Kilgreany Cave, Co. Waterford (89)	Castlepook Cave, Co. Cork (87)	Castletownroche Cave, Co. Cork (88)	Red Cellar Cave, Co. Limerick (86)	Alice and Gwendoline Caves	Catacombs	Newhall Caves	Barntick Cave	Coffey Cave	Plunkett Cave
Apodemus sylvaticus	×	×	×			×	×	×	×	×	×
Dicrostonyx torquatus	×	×	×	×	×	×	×	×		×	×
Lemmus lemmus			×	×							
Microtus agrestis		?									

Castletownroche Cave include mammoth, both mammoth and spotted hyaena being present in Castlepook Cave.

Although *Apodemus sylvaticus* has been recorded from several cave sites, Barrett-Hamilton & Hinton (1910–21) observed that in some instances it was most abundant in the upper layers, implying a possible late arrival in Ireland. Scharff *et al.* (1918), on the other hand, considered that at Castlepook Cave *Apodemus* was part of the Pleistocene fauna.

An imperfect skull of *Microtus agrestis* from Kilgreany Cave presents a problem, since this is the only possible fossil record of *Microtus* from Ireland, where this genus does not occur even at the present day. Savage (1966) observed that the skull is notably fresh and unaltered and drew attention to the occasional occurrence of vole skulls in north-east Ireland in owl pellets dropped by passing Scottish owls. There are no other records of *Microtus* in Ireland and the chance introduction of this specimen by owls or human activity needs to be taken into consideration.

D. Other Localities

(i) Cromerian localities. Stuart (1974) recorded *Mimomys* cf. *savini* associated with *Dicerorhinus* cf. *etruscus* from a site at Sugworth, near Oxford (21). He considered that the site is unlikely to be later than Cromerian.

(ii) Hoxnian localities. Carreck (1959) recorded *Pitymys* sp. from an interglacial tufa near Hitchin, Hertfordshire (39). This locality is unlikely to be later than Hoxnian in age. Other Hoxnian localities are Copford, Essex (42, Brown 1852 ; Turner 1970), with *Trogontherium boisvilletti*, and the Hoxnian type site of Hoxne with *Trogontherium boisvilletti* (Spencer 1956), *Apodemus* sp., *Lemmus* sp., *Arvicola* sp. and *Microtus* sp. (personal communication from Dr R. G. Wolff).

(iii) 'Ipswichian' localities. Six important East Anglian mammalian localities, usually regarded as of Ipswichian age (including the type Ipswichian locality, Bobbitshole) have produced rodent remains as shown in Table 11.

It has been claimed by Koenigswald (pers. comm.) that although the *Arvicola* from Barrington and from the Stuart collection from Swanton Morley (two hippopotamus localities) is *A. cantiana-terrestris* transition form, that from the Stuart collection from Stutton (a locality without hippopotamus) is *A. cantiana*, suggesting affinities with the Grays–Ilford–Aveley fauna of the Thames estuary. Stuart (1974), on the other hand, considers that the Barrington remains include both '*cantiana*' and '*terrestris*' and not merely intermediate forms, suggesting that the above interpretation is oversimplified. Stuart (*in litt.*) records *A. cantiana* from Harkstead, a locality near to and probably of the same age as Stutton.

Other 'Ipswichian' localities with rodent remains are Hessle (74) with *Arvicola* and Selsey (24) with *Castor*.

(iv) Last Glaciation localities. The Last Glaciation brings us within the range of radiocarbon dating. Four sites, two of them thus dated, will be mentioned here.

At Upton Warren, Worcestershire (20), remains of *Dicrostonyx* (determined by Carreck) were found in association with mammoth, woolly rhinoceros and reindeer

Distribution of rodent species at Bri

		Devon				Somerset					
	Ightham Fissures, Kent	Brixham Cave	Happaway Cave, Torquay	Levaton Cave, Torbryan	Chudleigh Fissure	Bleadon Cave	Uphill Cave	Hay Wood Rockshelter	Picken's Hole	Rowberrow Cavern	Aveline's Hole
*Sciurus vulgaris**								×			
Spermophilus superciliosus	×					×			×		
*Muscardinus avellanarius**											
*Castor fiber**								×			
Apodemus sylvaticus	×		×	×				×		×	×
*A. flavicollis**	×		×								×
*Rattus rattus**											×
Clethrionomys glareolus	×	×	×		×			×		×	×
Arvicola terrestris	×	×	×	×	×			×			×
Dicrostonyx torquatus	×				×					×	×
Lemmus lemmus	×				×		×				×
Microtus agrestis/arvalis group	×	×	×	×	×	×		×			×
M. oeconomus	×			×	×	×		×	×		×
M. gregalis	×	×	×		×	×	×		×		×
	Pleistocene megafauna and rodents with admixture of post-glacial sylvan elements	Associated Pleistocene megafauna	Probably mostly post-Pleistocene	Associated Pleistocene megafauna	Pleistocene microfauna	Pleistocene microfauna	Pleistocene microfauna	Holocene, confused strata	Upper Pleistocene megafauna	Pleistocene microfauna	Pleistocene megafauna and rodents with admixture of post-glacial rodents

* Probably post-Pleistocene.

st Glaciation and Holocene cave sites

ordshire		Derbyshire													
King Arthur's Cave	Merlin's Cave = ? Wye Cave	Harborough Cave	Langwith Cave	Dowel Cave		Etches' Cave		Fox Hole Cave		Pin Hole Cave	Elder Bush Cave, Staffordshire	Dog Holes Cave, Lancashire	Cowside Cave No. 3, Yorkshire	Gwaenysgor Cave, Flintshire	Lynx Cave, Denbighshire
Roman remains	Microfauna only	Post-Pleistocene	Associated Pleistocene megafauna	Late Pleistocene levels	Holocene levels	Late Pleistocene levels	Holocene levels	Late Pleistocene levels	Holocene (Beaker age) level	Pleistocene megafauna and rodents with admixture of post-glacial rodents	Upper Pleistocene megafauna	Pleistocene microfauna	Pleistocene microfauna	Associated Pleistocene megafauna	Associated probable late Palaeolithic and Romano-British remains
			×		×										
			×							×					
										×		×			
			×	×	×				×	×		×			×
					×		×			×					
			×												
	×		×	×	×		×		×	×	×	×		×	
	×		×	×	×	×	×		×	×	×	×	×		
×	×	×	×	×		×		×		×	×	×		×	×
	×		×	×		×				×	×	×			
×	×		×				×		×	×	×	×	×		×
×	×		×	×	×	×	×				×	×	×		×
×	×		×	×						×					

TABLE II

Rodent species from East Anglian 'Ipswichian' sites

	Suffolk					
	Stutton (47)	Harkstead (44)	Stoke Tunnel Beds (46)	Bobbitshole, Ipswich (46)	Barrington (40), Cambridgeshire	Swanton Morley (66), Norfolk
Apodemus sylvaticus	×			×		×
Clethrionomys cf. *glareolus*						×
Arvicola cantiana	×	×				
Arvicola cantiana-terrestris transition form			×		×	×
Arvicola sp.				×		
Microtus agrestis	×	×		×	×	
M. oeconomus		×				

List based on specimens in the Ipswich Museum (Stutton, Stoke Tunnel Beds, Harkstead and Bobbitshole), British Museum (Natural History) (Barrington), and Stuart Collection from Swanton Morley (Stuart 1974).

in terrace deposits of the River Salwarpe (Coope *et al.* 1961). Associated insect remains indicate cold continental conditions. There are ^{14}C dates of 41 500 ± 1200 years (GRO 595) and 41 900 ± 800 years (GRO 1245).

At Beckford, Worcestershire (19), remains which are probably *Microtus arvalis* have been determined by Dr G. B. Corbet from specimens separated by Coope from material collected by D. J. Briggs from deposits of the Carrant Brook, in a terrace equivalent to number 2 terrace of the Warwickshire Avon or the main terrace of the River Severn. Associated mammals include mammoth, woolly rhinoceros and horse. There is a cold insect fauna and ^{14}C dates of 27 650 ± 250 years (Birmingham 293) and 27 300 ± 500 (Birmingham 595).

At Fisherton, Wiltshire (22), *Dicrostonyx torquatus*, *Microtus oeconomus* and *Spermophilus superciliosus* were associated with remains of large Pleistocene mammals. In spite of earlier suggestions *Microtus nivalis* is absent. This is a typical Last Glaciation faunal assemblage.

At Brean Down, Somerset (9), remains of *Dicrostonyx* were found in association with arctic fox and reindeer in talus deposits regarded by Apsimon *et al.* (1961) as being of Late Glacial age (early Zone II).

(v) HOLOCENE LOCALITIES. Two rodent species, now extinct in the British Isles, survived into post-Pleistocene times. These are *Castor fiber* and *Microtus oeconomus*. Localities for *Castor fiber* include the Cambridge Fens (41), Staple Howe, Yorkshire

(75), Star Carr, Yorkshire (76), and Thatcham, Berkshire (23). *Microtus oeconomus* has been found in the Huntspill Cut (8) in the Somerset levels and on Nornour, Isles of Scilly (91).

(vi) Scottish localities. Other Scottish rodent finds include *Dicrostonyx* from Corstorphine, Edinburgh (81), and *Castor fiber* from the Loch of Marlee, Perthshire (82), and Middlestots Bog, Berwickshire (80). The various ages of these remains have not been determined.

III. CLASSIFICATION AND DISTRIBUTION OF RODENTS IN THE PLEISTOCENE OF THE BRITISH ISLES

In this section rodents represented in the British Pleistocene are discussed in systematic order. For completeness of taxonomic reference authors and dates of both families and genera are given, though these are generally omitted from the references. In the few cases where the currently used name of an extinct species is based on non-British material the original reference, marked **, is given in the synonymy. With these exceptions, only names used for fossil specimens from the British Isles are cited in the synonymy and each name is given only once, with reference to the first paper where it appeared. The type localities of extinct species of rodents are indicated * in the locality lists or, if non-British, in the sections on general distribution.

Locality lists for each species are divided into (a) English and Welsh, (b) Scottish and (c) Irish sites ; they are given in ascending stratigraphic order, as precisely as possible on the basis of current information. Where several records are believed to be of similar age they are grouped together, in alphabetical order, at the appropriate position. Numbers refer to site locations in Fig. 1. Published records at generic level only are generally not included in the locality lists. Though coverage is basically restricted to the Pleistocene, Holocene records of *Castor fiber* and *Microtus oeconomus* are also included since both these species are now extinct in the British Isles. Post-Pleistocene arrivals in the British Isles are briefly mentioned for the sake of completeness.

Family **SCIURIDAE** Brandt 1855

Genus ***SCIURUS*** Linnaeus 1758

Sciurus whitei Hinton 1914

Squirrel, extinct

1914 *Sciurus whitei* Hinton : 193–195, fig. 10.

Locality : *West Runton, Norfolk (65) : Hinton 1914.

Hinton described a new species of squirrel, *S. whitei*, from a unique fourth upper premolar (BM(NH), M 10720) from the marine 'Monkey Gravel' overlying the Cromerian Upper Freshwater Bed at West Runton, Norfolk.

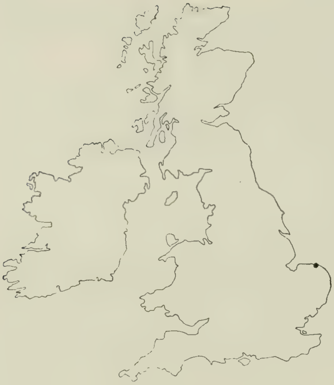


FIG. 5. Distribution of remains of *Sciurus whitei* Hinton in the British Isles.

No other fossil remains of this species have been found in the British Isles, though a number of fir cones from Cromerian deposits of the Forest Bed of Norfolk bear marks suggesting that they had been gnawed by squirrels (Newton 1882a). Newton (1881, 1882a, 1891) described and figured a humerus from Ostend, Norfolk (57), which agreed closely in form with that of the living red squirrel, *S. vulgaris* Linn., but he was not certain whether it came from the Forest Bed or from a Recent alluvial deposit.

On the continent of Europe, remains of *Sciurus* are known from a number of Early and Middle Pleistocene localities in France and Hungary, though they have usually been left without specific determination. Janossy (1962) discovered remains of a squirrel approaching *S. whitei* at the Middle Pleistocene locality of Tarkö in Hungary, and described them as belonging to a new subspecies, *S. whitei hungaricus* Janossy 1962. In his opinion *S. whitei* may represent an ancestral form of *S. vulgaris*.

Sciurus vulgaris Linnaeus 1758

Red squirrel

The red squirrel is a widespread Palaearctic species, still common in parts of the British Isles. It occurs principally in woodland, but also in scrub beyond the Arctic circle. Its remains have been found in Late Pleistocene sediments of Europe from France to the Ukraine, but are nowhere common.

There are no indisputable records of *S. vulgaris* in the Pleistocene of the British Isles. Its remains are known from Dowel and Langwith Caves, Derbyshire (71, 72 : Bramwell 1960, Mullins 1913). The Dowel Cave record is from a Holocene stratum. The stratigraphic position of the remains from Langwith Cave was not determined, but the occurrence of *Rattus rattus* Linn., the black rat, suggests that some Holocene mammalian remains were present in addition to the rich Pleistocene fauna of the cave.

Genus ***SPERMOPHILUS*** Cuvier 1825 [= *Citellus* Oken 1816][1]

It was long suspected that the ground squirrels of the British Pleistocene represent two species. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 724) wrote :

> Dr Forsyth Major studied the material [of ground-squirrels] with great care many years ago and we believe that he concluded that at least two species occur in the British Pleistocene ; unfortunately his results were never published. The writer in turn has made some progress with a similar investigation, but has not been able to complete his work yet. In his view also there are two species at least, both extinct, one being allied to the living *Citellus* [= *Spermophilus*] *erythrogenys*, the other more nearly related to *C.* [= *Spermophilus*] *eversmanni.*

Following studies of specimens from the British Museum (Natural History) the two forms have recently been distinguished by I. M. Gromov of Leningrad (*in litt.*) as *Citellus* [= *Spermophilus*] *superciliosus*, from the Upper Pleistocene, and *C.* [= *S.*] *primigenius* from deposits of earlier age.

Spermophilus (Urocitellus) primigenius Kormos 1934

Ground squirrel, extinct

1876 *Spermophilus* ; Cheadle : 70–71.
1882b *Spermophilus Altaicus* ? ; Newton : 51–54, pl. 2.
1885 *Spermophilus erythrogenoides* Falconer ; Lydekker : 212–213.
1934 ** *Spermophilus primigenius* Kormos : 314–315, fig. 45.
1947 *Citellus erythrogenoides* Falc. ; Jackson : 168.

LOCALITIES : Mundesley, Norfolk (60) : Newton 1882b.

Crayford and Erith, Kent (27) : Cheadle 1876, Lydekker 1885–87, Whitaker 1889, Newton 1890a, 1894, Barrett-Hamilton & Hinton 1910–21, Kennard 1944, Jackson 1947.

DISTRIBUTION IN THE BRITISH ISLES. Remains of this species of ground squirrel have been found abundantly in the Middle Terrace deposits of the Thames at Crayford and Erith, Kent. Cheadle (1876) attributed remains which he had found at Erith to *Spermophilus* sp. Subsequent writers (Lydekker, Whitaker, Newton, Barrett-Hamilton & Hinton, Kennard, Jackson) regarded the form represented at these localities as *S. erythrogenoides*. A skull from Erith was subsequently determined as *Citellus* [= *Spermophilus*] *primigenius* by Gromov, who wrote as follows (*in litt.*, translation) :

> Specimen M 9605, a deformed skull with a fragment of mandible, belongs to a large form of *Citellus* (*Urocitellus*) *primigenius* Korm., approaching in its dimensions the Polish *C.* (*U.*) *polonicus* Gromov, though it preserves the basic characters of the former. The skull also has some characters typical for *C. nogaici* Top. : a well-marked basin which divides the hypo- and entoconid parts on the grinding surface of M_3, a weakly developed posterior crest on M^3, a weakly developed narrowing on the hypoconid of P_4, and a *foramen mentale* shifted upwards. The second of these characters, as well as the presence of tiny cusps on the bottom of the

---

[1] Although the name *Citellus* Oken 1816 has been extensively used hitherto for these ground squirrels, Oken (1815–16) is not consistently binominal (Ellerman & Morrison-Scott 1966 : 3) and was rejected as unavailable by fiat of the International Commission on Zoological Nomenclature (Opinion 417, 1956).

external valleys of M_1–M_3, occurs also in *C. polonicus*. Finally, peculiar to the British remains is the forward shifting of the crests of the masseteric plate on the mandible. It is probably a distinct subspecies.

Some isolated worn teeth of *Spermophilus* described by Newton (1882b : 54) as close to *S. altaicus* (= *S. eversmanni*) were found in deposits now regarded as of early Anglian age at Mundesley, Norfolk. They provide the earliest record of *Spermophilus* in the British Isles and are provisionally referred to *S.* (*Urocitellus*) *primigenius*.

GENERAL DISTRIBUTION. *S. primigenius* (type locality Kalkberg, Nagyhársanyberg) is known from Villafranchian as well as from later (Günz, Günz–Mindel) deposits of Hungary. It is also present in the Middle Pleistocene of the Ukraine and Germany (Gromov 1965). According to Chaline (1972), ground squirrels, which he was unable to determine specifically, were present during the Mindel and Riss glaciations in France.

The living representatives of the subgenus *Urocitellus* – the long-tailed ground squirrels *S. undulatus* (Pallas 1779) and *S. parryi* Richardson 1827 – inhabit steppes as well as meadows in the tundra-zone of central and eastern Asia and North America.

Spermophilus (Colobotis) superciliosus (Kaup 1839)

Ground squirrel, extinct

1839	** *Spermophilus superciliosus* Kaup : 112.
1866	*Spermophilus erythrogenoides* (Falc.) ; Dawkins & Sanford : xxxix (nomen nudum).
1866	*Spermophilus citillus* Pallas ; Dawkins & Sanford : xxxix.
1868	*Spermophilus erythrogenoides* ; Falconer, in Murchison : 452–454, pl. 35.
1974	*Citellus* sp. ; Stuart : 246.

LOCALITIES : Langwith Cave, Derbyshire (72) : Mullins 1913, Barrett-Hamilton & Hinton 1910–21.

Mendip Hills Caves (Bleadon Cave and others) : Dawkins & Sanford 1866, Falconer 1868, Stevens 1869, Sanford 1870a, b, Newton 1882a, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Fisherton, Wiltshire (22) : Falconer 1868, Stevens 1869, Barrett-Hamilton & Hinton 1910–21.

Ightham Fissures, Kent (28) : Newton 1894, 1899b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Picken's Hole (layer 3), Somerset (10) : Stuart (1974).

Pin Hole Cave, Derbyshire (73) : Jackson 1947.

DISTRIBUTION IN THE BRITISH ISLES. *S. superciliosus* is a characteristic element of the fauna of the Last Glaciation.

GENERAL DISTRIBUTION AND SYSTEMATIC REMARKS. *S. superciliosus* was described by Kaup from Eppelsheim in Germany. It is an element of the Late Pleistocene (Würm) fauna, present in almost the whole of Europe, including France, Germany, Poland, the European and Asiatic part of the Soviet Union, Czechoslovakia and Hungary. Its living relatives inhabit the steppe zone of eastern Europe and Asia.

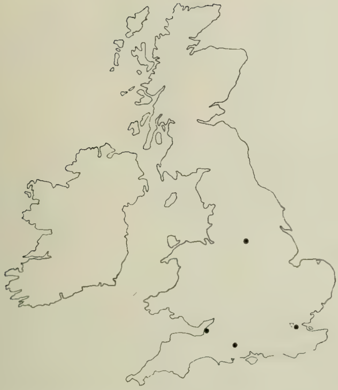


FIG. 6. Distribution of remains of *Spermophilus* (*Urocitellus*) *primigenius* Kormos (▽) and *S.* (*Colobotis*) *superciliosus* (Kaup) (●) in the British Isles.

In Britain it has usually been recorded as *S. erythrogenoides*, a name first used by Falconer (in Murchison 1868) for remains from caves of the Mendip Hills. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 723) stated that recent study tended to show that this name must be treated as a synonym of *S. superciliosus*.

I. M. Gromov of Leningrad studied the specimens from Ightham Fissures, Kent, and made the following remarks (*in litt.*, translation) :

> Two mandibular rami, no. M 11867, are typical remains of *Citellus* (*Colobotis*) *superciliosus* Kaup, broadly distributed in the northern part of continental Europe in Late Pleistocene ; during some part of this time it evidently also inhabited the British Isles. From the characteristic features of this species, as shown by the above-mentioned material, the following can be stated : width of P_4 no more than 11 per cent greater than its length, *processus articularis* short and broad below the head, posterior incision of the mandible relatively small, *foramen mentale* situated far from the anterior border of the masseteric plates, etc.

Family **GLIRIDAE** Thomas 1897

Genus ***MUSCARDINUS*** Kaup 1829

Hinton (in Barrett-Hamilton & Hinton 1910–21 : 351) recorded a single tooth of *Muscardinus* from the Forest Bed of Norfolk. This specimen has not been seen by the present writers. *Muscardinus* is nevertheless known from some Cromerian localities on the European continent so that its presence in Britain in Cromerian times is not improbable.

Muscardinus avellanarius (Linnaeus 1758)

Common or hazel dormouse

Although remains of this species have been found at a number of cave sites – Dog Holes and Pin Hole Caves (79, 73) : Jackson (1934, 1947) ; Great Doward Cave (17) : British Museum (Natural History) – all these remains are probably of Holocene age.

The hazel dormouse is now distributed in southern, western and central Europe, including southern Sweden and Britain, and in Asia Minor. On the continent of Europe it has been found in interglacial deposits as early as Tiglian. It was also present in France during the last interglacial (Chaline 1972).

Family **CASTORIDAE** Gray 1821

Genus ***TROGONTHERIUM*** Fischer 1809

Trogontherium minus Newton 1890

Giant beaver, extinct

1890b *Trogontherium minus* Newton : 447–448.

LOCALITIES : Red Crag of Felixstowe and *Woodbridge, Suffolk (45, 47) : Newton 1890b, 1891, 1902, Barrett-Hamilton & Hinton 1910–21, Schreuder 1929, 1951.

According to Schreuder (1951), who made a very thorough study of the genus *Trogontherium*, this species is more primitive than the other representatives of the genus, *T. cuvieri* Fischer and *T. boisvilleti* (Laugel).

T. minus is also known from Astian (Pliocene) sediments of Perpignan, France. The Red Crag specimens (like many other Crag fossils) are probably derived from earlier deposits and cannot be regarded as part of the contemporary Lower Pleistocene fauna.

Trogontherium boisvilletti (Laugel 1862)

Giant beaver, extinct

1846 *Trogontherium Cuvieri* ; Owen : 184–189, figs 71–73.
1848 *Diabroticus Schmerlingi* ; Pomel : 167.
1862 ** *Conodontes Boisvilletti* Laugel : 715–718.
1866 *Castor trogontherium* Cuvier ; Dawkins & Sanford : xxxvi.
1902 *Dipoides Lydekkeri* Schlosser : 117.
1951 *Trogontherium boisvilletti* Laugel ; Schreuder : 403.
1956 *Trogontherium* sp. ; Spencer : 354.

LOCALITIES : Sizewell, Suffolk, and Thorpe, Norfolk[1] (49, 48, Norwich Crag) : Lydekker 1885, Schreuder 1951.

East Runton (64, Pastonian Forest Bed) : Newton 1882a, 1892, Barrett-Hamilton & Hinton 1910–21, Schreuder 1951.

Bacton, Cromer, Kessingland, Mundesley, Overstrand, Paston and West Runton (58, 63, 52, 60, 62, 59, 65, 'Cromerian') : Lyell 1840, Owen 1846, Dawkins & Sanford 1866, Owen 1869, Newton 1881, 1882a, Lydekker 1885, Reid 1890, Hinton 1914, Schreuder 1929, 1931.

Clacton, Copford, Hoxne and Swanscombe (43, 42, 54, 30, Hoxnian) : Brown 1852, Newton 1902, Schlosser 1902, Stopes 1904, Newton 1916, Schreuder 1929, 1951, Spencer 1956, Sutcliffe 1964, Singer *et al.* 1973.

RANGE : *T. boisvilletti* was apparently present in Britain during the Tiglian, Cromerian and Hoxnian. Its remains have been found frequently in deposits of

---

[1] See also footnote on p. 96.

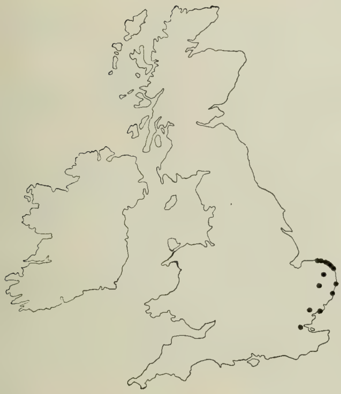


FIG. 7. Distribution of remains of *Trogontherium boisvilletti* (Laugel) in the British Isles.

the Norfolk Forest Bed ; only a few Hoxnian specimens are known. These are a solitary incisor from Ingress Vale, Swanscombe (Newton 1902, Stopes 1904, Schreuder 1929, 1951, Sutcliffe 1964), a cheek tooth from Copford (Brown 1852, site dated as Hoxnian by Turner 1970, BM(NH) 27985), a femur and eight cheek teeth from Hoxne (Spencer 1956) ; and part of a skull from Clacton (Singer *et al.* 1973).

GENERAL DISTRIBUTION. *T. boisvilletti* is known from the early Pleistocene in Britain, Holland, France (type locality Saint-Prest, near Chartres) and western parts of Germany. Further to the east it is, according to Schreuder (1951), replaced by a slightly different species, *T. cuvieri* Fischer, first described from the border of the Azov Sea. *T. cuvieri* was present in Germany during the Holsteinian Interglacial. According to Lehmann (1953), *T. cuvieri* is a more advanced species than *T. boisvilletti* and may be its descendant. If this is true, the British Hoxnian remains may represent *T. cuvieri*, but there are too few suitable specimens to allow a detailed determination.

Genus ***CASTOR*** Linnaeus 1758

Castor fiber Linnaeus 1758

Beaver

1846	*Castor europaeus* ; Owen : 190–200, figs 74–75.
1864	*Castor veterior* Lankester : 355–356.
1889	*Castor fiber* Linn. (= *europaeus* Owen) ; Whitaker : 336.
1908b	*Castor plicidens* Maj. ; Major : 630–635, figs 132–136.
1964	*Castor* sp. ; Spencer : 338.

LOCALITIES : Sutton and Woodbridge, Suffolk (47, Red Crag) : Lankester 1864, Newton 1891, Barrett-Hamilton & Hinton 1910–21, Schreuder 1929.

East Runton (64, Pastonian Forest Bed) : Major 1908b.

Bacton, Kessingland, Mundesley, West Runton (58, 52, 60, 65, Forest Bed) : Dawkins & Sanford 1866, Owen 1869, Newton 1881, 1882a, 1891, Major 1908b, Barrett-Hamilton & Hinton 1910–21, Hinton 1914, Schreuder 1929, 1931, Friant 1962.

Westbury-sub-Mendip Fissure (13, lower middle Pleistocene) : Bishop 1974.

Clacton (43, Hoxnian) : Barrett-Hamilton & Hinton 1910–21, Hinton 1923b, Sutcliffe 1964.

Swanscombe (Barnfield Pit), Kent (30, Hoxnian) : BM(NH).

Grays Thurrock and Ilford, Essex (33, 35) : Lankester 1864, Dawkins & Sanford 1866, Whitaker 1889, Hinton 1900b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Selsey, Sussex and Upnor, Kent (24, 31, Last Interglacial) : BM(NH).

Kent's Cavern, Devon (6) : BM(NH).

Cambridge Fens, Cambridgeshire ; Hay Wood Rockshelter, Somerset ; Staple Howe, Yorkshire ; Star Carr, Yorkshire ; Thatcham, Berks (41, 10, 75, 76, 23, Holocene) : Montagu 1924, Brewster 1963, Fraser & King 1954, Wymer 1962.

Loch of Marlee, Perthshire, and Middlestots Bog, Edrom Parish, Berwickshire (82, 80) : Barrett-Hamilton & Hinton 1910–21.

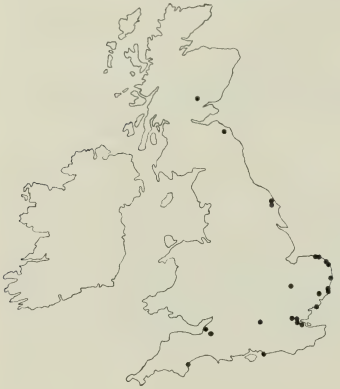


Fig. 8. Distribution of fossil remains of *Castor fiber* Linn. in the British Isles.

Range. Remains of *C. fiber* have been found in deposits in the British Isles ranging in age from lowest Pleistocene (Red Crag) to Holocene. The species spread to Scotland but apparently never reached Ireland. Barrett-Hamilton & Hinton (1910–21) considered that the beaver did not become extinct in Britain before the thirteenth century A.D.

General distribution. Although limited to a small number of relict localities as a result of extermination by man, *C. fiber* is still widely distributed in Europe and Asia. Its fossil remains are known from the Pliocene and Pleistocene of Europe and Asia.

Systematic remarks. The beaver remains from the Red Crag were described by Lankester (1864) under the new name *C. veterior*. Newton (1891) considered that this species was conspecific with *C. fiber* and Schreuder (1929) proved it by a detailed comparison. C. I. F. Major (1908a) described some remains from the Forest Bed at East Runton as belonging to *C. plicidens*, a species described by him from Val d'Arno in Italy. Schreuder (1929) showed that the folding of tooth-enamel is a character depending upon the individual age of the animal and *C. plicidens* is therefore a synonym of *C. fiber*. Later it was found that individuals of '*C. plicidens*' sometimes appear among postglacial beavers. Viret (1954), however, studying the skull of a Villafranchian beaver from St Vallier in France, found some morphological differences from the Recent beaver and was inclined to retain the name *C. plicidens* for all the beavers from that period, not only for specimens with folded enamel. According to Lehmann (1957) these differences are rather of a subspecific character and he designated the Villafranchian beavers as '*Castor fiber plicidens* Major 1875'. Until statistical analysis of the variability of the living beaver has been made, it seems preferable to use only the specific name *Castor fiber* Linn. for the Astian (Upper Pliocene) as well as for the Pleistocene beavers.

Family **MURIDAE** Gray 1821

Genus ***APODEMUS*** Kaup 1829

Apodemus sylvaticus (Linnaeus 1758)

Wood mouse

1846 *Mus musculus* (?) ; Owen : 209, fig. 79.
1881 *Mus sylvaticus* ; Newton : 258–259.
1910 *Micromys* (= *Mus*) *sylvaticus* (Linné) ; Jackson : 328.
1910b *Mus* sp., allied to *M. sylvaticus* ; Hinton : 489–507.
1915 *Apodemus* sp. ; Hinton : 580.
1915 *Apodemus whitei* Hinton : 580–581.
1915 *Apodemus sylvaticus* L. ; Hinton : 581–582.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1881, 1882a, 1891, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, BM(NH).

Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974.

Hitchin, Hertfordshire (39) : Carreck 1959.

Swanscombe (Ingress Vale), Kent (30) : Stopes 1904, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, Sutcliffe 1964, BM(NH).

Hoxne, Suffolk (54) : Wolff (*in litt.*, *Apodemus* sp.).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1915.

Stutton, Suffolk (44) : Stuart 1974 (*A. sylvaticus* group).

Bacon Hole, Glamorganshire (16) : det. A. J. Stuart (*in litt.*).

Kirkdale Cave, Yorkshire (77) : Owen 1846, Dawkins & Sanford 1866.

Swanton Morley, Norfolk (66) : Stuart 1974 (*A. sylvaticus* group).

Tornewton Cave, Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, BM(NH).

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Gwaenysgor Cave, Flintshire (68) : Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Barrett-Hamilton & Hinton 1910–21, Hinton 1915, Carreck 1957, BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913.

Levaton Cave, Devon (2) : Carreck 1957.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Rowberrow Cavern, Somerset (11) : BM(NH).

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Happaway Cave, Devon (5) : BM(NH).

Lynx Cave, Denbighshire (67) : Blore 1966.

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Joint Mitnor Cave, Devon (1, Layer 10, Holocene) : BM(NH).

Ballynamintra Cave, Co. Waterford (90) : Barrett-Hamilton & Hinton 1910–21, Jackson 1929b.

Castlepook Cave, Co. Cork (87) : Scharff, Seymour & Newton 1918, BM(NH).

Edenvale Caves (Alice and Gwendoline, Catacombs, Newhall, Barntick), Co. Clare (85) : Barrett-Hamilton & Hinton 1910–21, Scharff 1906.

Keshcorran Caves (Coffey, Plunkett), Co. Sligo (84) : Barrett-Hamilton & Hinton 1910–21, Jackson 1929b, Scharff *et al.* 1903.

Kilgreany Cave, Co. Waterford (89) : Jackson 1929b.

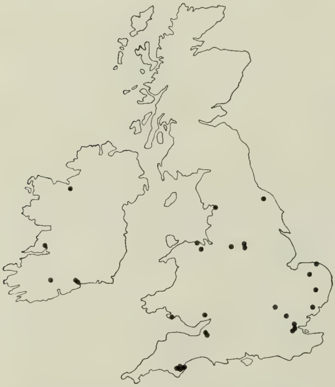


Fig. 9. Distribution of fossil remains of *Apodemus sylvaticus* (Linn.) in the British Isles.

Distribution in the British Isles. *A. sylvaticus* was present in the British Isles during the Cromerian, Hoxnian and Ipswichian interglacials. It probably disappeared from the country at the time of the cold stage represented by the Tornewton Cave Glutton Stratum. A solitary specimen from this deposit may have been introduced from a higher, interglacial, level. This species was present during the Last Glaciation and during the Holocene. Most of the localities, especially caves, cannot be accurately dated, and it is difficult to decide if *A. sylvaticus* was present throughout the Holocene without interruption. It may have reached Ireland during Upper Pleistocene times.

General distribution. *A. sylvaticus* is now widely distributed in Europe, north Africa and western Asia. The fossil remains of this or nearly related species are known from the Pleistocene of Europe and China. The oldest of them are dated as Tiglian, with further records from deposits of Cromerian, Holsteinian and later date.

Systematic remarks. Hinton (1915 : 580) referred the teeth from the Cromerian Upper Freshwater deposits of West Runton to *Apodemus* sp. Although he found that their pattern was indistinguishable from that of *A. sylvaticus* he considered that the material was insufficient for fine determination. From Swanscombe (Ingress Vale) (*loc. cit.*) he described a new species, which he named *A. whitei*, from part of a maxilla differing slightly from recent specimens of *A. sylvaticus*. However, the characters concerned lie within the range of individual variability and there does not seem to be any good reason for regarding the West Runton form as a distinct species.

Apodemus flavicollis (Melchior 1834)

Yellow-necked mouse

1894	*Mus Abbotti* Newton : 195, pl. xi, fig. 8 (not *M. abbotti* Waterhouse).
1899a	*Mus Lewisi* Newton : 381.
1915	*Apodemus lewisi* Newton ; Hinton : 582–584.
1921	*Apodemus Flavicollis* Melchior ; Hinton : 78.

Localities : Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924.
Dowel Cave, Derbyshire (71) : Bramwell 1960.
Etches' Cave, Derbyshire (71) : Pernetta 1966.
Happaway Cave, Devon (5) : Hinton 1915, BM(NH).
Ightham Fissures, Kent (28) : Newton 1894, 1899a, b, Hinton 1915, BM(NH).
Kent's Cavern, Devon (6) : Hinton 1915.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Distribution in the British Isles. Remains of *A. flavicollis* have been found almost exclusively in very late sediments. Many of the records must nevertheless be considered doubtful in view of the great difficulty in distinguishing remains of this species from those of *A. sylvaticus*. The remains recorded from Dowel Cave were found in a Neolithic layer (Bramwell 1960 : [10]–pages unnumbered) and those from Etches' Cave were in early postglacial layers (Pernetta 1966 : 12, 15). Hinton (1921) considered that the Aveline's Hole remains were probably a late introduction. The same may be true for the Ightham Fissures. The Kent's Cavern and Happaway specimens were excavated a century ago. From Pin Hole Cave, Derbyshire (Jackson 1934), remains of *A. flavicollis* have been recorded from both the superficial levels and at a depth of more than 3 m (10 ft), where they were apparently associated with Upper Pleistocene faunal remains.

General distribution. At the present time *A. flavicollis* is widespread in Europe and east as far as the Urals and Caucasus. It is absent from a large part of western Europe (France, Belgium, Holland), but is present in England and southern Sweden. Nothing is known about the fossil remains. It is absent from the Pleistocene of France (Chaline 1972). It is difficult to decide whether this species represents a natural migration at the end of Pleistocene or during the Holocene or whether it was brought by man.

SYSTEMATIC REMARKS. According to Hinton (1915), *A. lewisi*, described from the Ightham Fissures by Newton (1899a, b), is closely related to, if not identical with, *A. flavicollis* Melchior. Jackson (1934) determined his material as '*A. flavicollis* (= *A. lewisi*)'. The lack of an anterior accessory cusp on M_1 is, according to Hinton (1915), of no significance in specific determination, because the cusp is apparently absent in slightly worn teeth of *A. flavicollis*. It seems probable that the holotype of *A. lewisi* is nothing but a Recent specimen of *A. flavicollis*.

Genus ***MICROMYS*** Dehm 1841

Micromys minutus (Pallas 1771)

Harvest mouse

This species was probably introduced into Britain by man in postglacial times. According to Barrett-Hamilton & Hinton (1910–21) it is unknown there in a fossil state. Remains found at Tornewton Cave (Kowalski 1967) are from a surface fissure unconnected with the main sequence of deposits and are unlikely to be of any antiquity.

M. minutus, now widely distributed in Europe and Asia, is present in England and perhaps in the southern parts of Scotland. The genus *Micromys*, and probably the Recent species, is known in continental Europe from the late Pleistocene.

Genus ***MUS*** Linnaeus 1758

Mus musculus Linnaeus 1758

House mouse

The house mouse was introduced into Britain by man. Barrett-Hamilton & Hinton (1910–21) discussed some early data about its fossil occurrence in Britain and considered that all are erroneous or refer to Recent remains. There is no evidence for the occurrence of the house mouse in Britain before the Iron Age.

Genus ***RATTUS*** Fischer 1803

Rattus rattus (Linnaeus 1758)

Black rat

Although remains of the black rat have been recorded from Aveline's Hole (Hinton 1921) and Langwith Cave (Mullins 1913) these are probably Recent. The black rat was introduced into the British Isles by man during the historical period.

Rattus norvegicus (Berkenhout 1769)

Brown rat

The brown rat is a recent addition to the British mammalian fauna. Jackson (1929b) records its remains from Kilgreany Cave, Ireland, in an upper layer with remains of domestic animals and prehistoric material, but these are probably of very recent date.

Family **CRICETIDAE** Rochebrune 1883

Genus ***CRICETUS*** Leske 1779

Cricetus cricetus (Linnaeus 1758)

Common hamster

1909 *Cricetus vulgaris Runtonensis* Newton : 110–113, fig. (unnumbered).
1967 *Cricetus cricetus* (Linnaeus 1758) ; Kowalski : 119–120.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1909, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Osborn 1922, BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

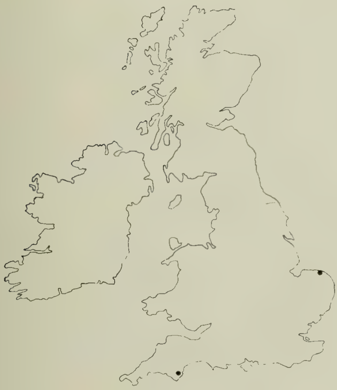


FIG. 10. Distribution of fossil remains of *Cricetus cricetus* (Linn.) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. Representatives of the genus *Cricetus* appeared twice in Britain : in the Cromerian interglacial and during the cold stage represented by the Tornewton Cave Glutton Stratum. The Tornewton Cave remains represent at least two individuals.

GENERAL DISTRIBUTION. *C. cricetus*, the only living member of its genus, occurs at the present time in eastern Europe and in the western part of Asia. It is also present in western and central Europe where its range is insular and seems to be characterized by gradually increasing expansion. It occurs in steppes, parklands and meadows. In Europe its occurrence is now associated with arable fields. Fossil remains of *Cricetus* are known from the early, middle and late Pleistocene of western, central and eastern Europe, especially in deposits indicating a cold and arid environment.

SYSTEMATIC REMARKS. All the fossil remains of the genus *Cricetus* are very uniform in their dental morphology and do not differ from the Recent ones. They do, however, vary greatly in size. On this basis many new forms have been described, some under specific, others under subspecific names. The specimen from the Cromer Forest Bed, BM(NH) M18352, an upper jaw with a tooth-row 9·3 mm long, is the holotype of a form known as *Cricetus runtonensis* or *C. cricetus runtonensis*. According to Schaub (1930), it is a synonym of *C. c. major* Woldřich described from the late Pleistocene deposits of Czechoslovakia. Other palaeontologists use the name *C. runtonensis* to designate larger representatives of *Cricetus* from the early Pleistocene, usually without giving sufficient morphological reasons for its distinctness from later populations. According to Fahlbusch (1969), there are some peculiarities in the pattern of M_2 in *C. runtonensis*, but a similar morphology can also be found in some Recent specimens. In the opinion of one of us (K. K.) the large early Pleistocene hamsters are at most subspecifically distinct from those of the late Pleistocene and present day. The great variability of this species in the Pleistocene was connected with changing climatic conditions.

Genus ***ALLOCRICETUS*** Schaub 1930

cf. ***Allocricetus bursae*** Schaub 1930

Hamster, extinct

1870a	*Cricetus songarus* ; Sanford : 51, 56, fig. 6.
1870b	*Cricetus* (*Mus*) *songarus* (Pallas) ; Sanford : 128–129 ; pl. viii, fig. 6.
1913	*Phodopus sanfordi* Hinton, in Barrett-Hamilton & Hinton 1910–21 : 383, fig. 53.
1967	*Phodopus songorus* (Pallas) ; Kowalski : 113–114.

LOCALITIES : Hutton Cave, Somerset (10) : Sanford 1870a, b, Newton 1909, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

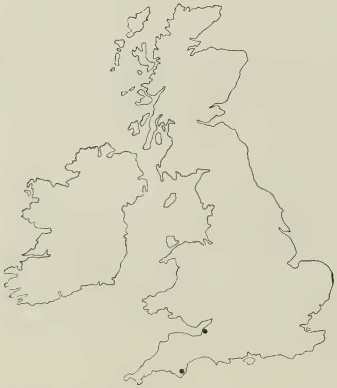


FIG. 11. Distribution of remains of cf. *Allocricetus bursae* Schaub in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. The occurrence of this species in the Glutton Stratum of Tornewton Cave shows that it was present during the pre-hippopotamus cold stage represented by this deposit. Although the age of the Hutton Cave fauna is unknown, the occurrence of remains of a relatively primitive form of mammoth suggests that this record is at least as early as that from Tornewton Cave.

General distribution and systematic remarks. Small representatives of Cricetidae are common in the early, middle and late Pleistocene of Europe. The uniform structure of the teeth in Cricetidae makes the systematic determination of their remains very difficult. According to Schaub (1930), the small hamsters of the late Pleistocene of Europe should be referred to *Phodopus songorus*. Janossy (1961) later stated that Schaub based his determination on incorrectly determined Recent specimens and claimed that the small hamster described by him is conspecific with Recent *Cricetulus migratorius*. The same name was used for English specimens by Kurtén (1969). Chaline (1972) did not find this species in France, but determined all late Pleistocene small French hamsters as *Allocricetus bursae* Schaub 1930. A more detailed study of English specimens will be necessary before it is possible to decide whether they belong to one or two species and what species there are.

In the earliest description of British hamster remains (those from Hutton), Sanford (1870) applied the name *Cricetus songarus*. Hinton (in Barrett-Hamilton & Hinton 1910–21 : 383) considered that the remains should be placed in the genus *Phodopus* and that they could not be synonymized with *P. songorus* but needed a new name, for which he proposed *P. sanfordi*. No reasons for this decision are given. If the British specimens are conspecific with *A. bursae* Schaub then this name is a junior synonym of *P. sanfordi* Hinton and must be replaced by it.

Small hamsters are now an element of the steppe fauna, and their species are broadly distributed in south-eastern Europe as well as in western and central Asia. *C. migratorius* ranges from south-eastern Europe to China. This species, partly cited under the name of *A. bursae* Schaub, is known as a fossil from the late Pleistocene of Germany, Switzerland, Spain, France, Czechoslovakia, Hungary, Poland and the Soviet Union.

Genus ***DICROSTONYX*** Gloger 1841

Dicrostonyx torquatus (Pallas 1779)

Collared lemming

1869	*Lemmus torquatus* ; Stevens : 110, 113.
1870a	*Arvicola Gulielmi* Sanford : 51, 55, fig. 2.
1870b	*Arvicola Gulielmi* Sanford : 125, pl. viii, fig. 2.
1874	*Myodes torquatus* Pall. ; Blackmore & Alston : 469–470.
1910a	*Dicrostonyx gulielmi* Sanford ; Hinton : 38–39.
1910a	*Dicrostonyx henseli* Hinton : 37–38.
1960	*Dicrostonyx* sp. ; Bramwell : [10].

Localities : Westbury-sub-Mendip, Somerset (13) (*Dicrostonyx* sp., lower middle Pleistocene) : Bishop 1974.

Erith, Kent (27) : Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947.

Hutton Cave, Somerset (10) : Stevens 1869, Sanford 1870a, b, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Tornewton Cave (Glutton Stratum and Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : Hinton 1926b.

Dog Holes Cave, Lancashire (79) : Jackson 1909, 1910, 1929a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1947, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Fisherton, Wiltshire (22) : Stevens 1869, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Gwaenysgor Cave, Flintshire (68) : Jackson 1932 (*fide* Jackson 1947), Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Jackson 1909, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929a, 1947, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : BM(NH).

King Arthur's Cave, Herefordshire (17) : BM(NH) (Hinton collection).

Langwith Cave, Derbyshire (72) : Mullins 1913, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929a, 1947, BM(NH).

Merlin's Cave, Herefordshire (18) : Hinton 1925, 1926b, BM(NH).

Murston, Kent (32) : Newton 1890a, Barrett-Hamilton & Hinton 1910–21.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Rowberrow Cavern, Somerset (11) : BM(NH) (Hinton collection).

Upton Warren, Worcestershire (20) : Coope *et al.* 1961.

Brean Down, Somerset (9) : Apsimon *et al.* 1961.

Fox Hole Cave, Derbyshire (71) : Bramwell 1970.

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Lynx Cave, Denbighshire (67) : Blore 1966.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Hackney, London (36) : BM(NH).

Angel Road, Middlesex (36) : Hinton 1912, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Ponders End, Middlesex (36) : Hinton 1926b.

Corstorphine, nr. Edinburgh, Scotland (81) : Evans 1907, 1913, Barrett-Hamilton & Hinton 1910–21, Jackson 1929b.

Creag nan Uamh Cave, Sutherland (83) : Peach & Horne 1917.

Ballynamintra Cave, Co. Waterford, Ireland (90) : Coleman 1965.

Castlepook Cave, Co. Cork (87) : Ussher *et al.* 1908, Jackson 1910, Ussher 1910, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929b, 1947, Coleman 1965.

Castletownroche Cave, Co. Cork (88) : Coleman 1965.

Edenvale Caves (Alice and Gwendoline, Catacombs, Newhall), Co. Clare (85) : Scharff 1906, Hinton 1926b, Coleman 1965, BM(NH).

Keshcorran Caves (Coffey, Plunkett), Co. Sligo (84) : Jackson 1909, Scharff *et al.* 1903, Scharff, Seymour & Newton 1918, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Jackson 1929b, Coleman 1965, BM(NH).

Kilgreany Cave, Co. Waterford (89) : Jackson 1929b, Coleman 1965.

Red Cellar Cave, Co. Limerick (86) : Coleman 1965.

Brandon, Warwickshire, and Penkridge, Staffordshire, are two additional *Dicrostonyx* localities not marked on Fig. 1, which were notified to us by Mr J. Carreck (*in litt.*) after the compilation of the above list.

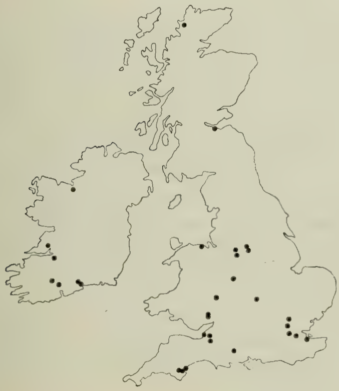


FIG. 12. Distribution of fossil remains of *Dicrostonyx torquatus* (Pallas) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *Dicrostonyx* is known in the British Isles from at least three stages of the Pleistocene. The earliest record (*Dicrostonyx* sp.) is from the lower middle Pleistocene site of Westbury-sub-Mendip. The second stage is represented by remains from the *Corbicula* bed at Erith and the Glutton Stratum of Tornewton Cave. At the last-mentioned site *Dicrostonyx* disappeared in the overlying Last Interglacial deposits and reappeared again in the Last Glaciation Reindeer Stratum. During the Last Glaciation it reached its greatest climax, spreading throughout England, Wales, Scotland and Ireland. Its remains are especially abundant in deposits dating from the later part of this stage and it was clearly a dominant element of the tundra faunal assemblage of that time. At Nazeing, Essex, it apparently survived until late Glacial pollen Zone III.

GENERAL DISTRIBUTION. The collared lemming is now widely distributed in the tundra belt of the Holarctic, in both Eurasia and North America. The American subspecies are sometimes recognized as specifically different from those of Eurasia. Fossil remains are known from the deposits of four different glaciations in Europe and they are also present in Asia and North America. Pre-Cromerian collared lemmings from Czechoslovakia and Poland are morphologically different from later ones and were named *Dicrostonyx simplicior* Fejfar 1966. During the Last Glaciation *D. torquatus* in Europe reached as far south as Hungary, Switzerland and central France.

SYSTEMATIC REMARKS. Hinton (1910a) distinguished two species of fossil collared lemmings in the British Isles, *Dicrostonyx gulielmi* and *D. henseli*. According to him the differences between these were as great as those between different Recent species of the genus *Dicrostonyx*. It is now generally accepted, however, that disregarding the Canadian *D. hudsonius* (which does not concern us here) all living forms belong to one species. The European fossil forms may, at the most, be subspecifically different from Recent ones, but this seems not to be the case as the two forms described by Hinton are present together at nearly all localities. Janossy (1954) found in Hungarian caves not only all possible intermediate forms between *D. gulielmi* and *D. henseli*, but also specimens with left tooth-row of one type and right one of the other. Most palaeontologists are of the opinion that there was only one species of the collared lemming in the Upper Pleistocene of Europe and that it was conspecific with the living *D. torquatus*. Like the Recent population, it was very variable (Mandach 1938). Recently Agadzhanian (1973) has stated that, among the populations of Recent and fossil collared lemmings, there are different morphotypes, differing in the grade of complication of the crown pattern of their molars. He considered that the simpler morphotypes are more numerous among the populations from the Last Glaciation of Eurasia than among Recent animals from north Asia. For this reason he favoured preserving the name *D. gulielmi* as the oldest available designation for the collared lemmings from the time of the Last Glaciation of Eurasia.

Genus ***LEMMUS*** Link 1795

Lemmus lemmus (Linnaeus 1758)

Norwegian lemming

1870a	*Lemmus norvegicus* (var.) ; Sanford : 51, 56, fig. 4.
1870b	*Lemmus norvegicus* ; Sanford : 125–126, pl. viii, fig. 4.
1874	*Myodes lemmus* (Linn.) ; Blackmore & Alston : 470–471.
1921	*Lemmus lemmus* Linn. ; Hinton : 75–76.
1950	*Lemmus* sp. ; Schreuder : 629, 633–634.

LOCALITIES : Westbury-sub-Mendip, Somerset (13) (*Lemmus* sp., lower middle Pleistocene) : Bishop 1974.

Hoxne, Suffolk (54) : Wolff (*in litt.*).

Swanscombe (Barnfield Pit, Upper Middle Gravel), Kent (30) (*Lemmus* sp.) : Schreuder 1950.

Erith, Kent (27) : Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, BM(NH).

Hutton Cave, Somerset (10) : Sanford 1870a, b, Blackmore & Alston 1874, Jackson 1909, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : Hinton 1926b.

Dog Holes Cave, Lancashire (79) : Jackson 1909, 1910, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Great Doward Cave, Herefordshire (17) : Bristol University Spelaeological Society, det. K. K.

Ightham Fissures, Kent (28) : Newton 1894, Bate 1901, Jackson 1909, Hinton 1910a, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : Kennard 1945–46.

Langwith Cave, Derbyshire (72) : Mullins 1913, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b.

Merlin's Cave, Herefordshire (18) : Hinton 1924, 1926b, BM(NH).

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Uphill Cave, Somerset (9) : Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, BM(NH).

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Harborough Cave, Derbyshire (70) : Jackson 1929a.

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Castlepook Cave, Co. Cork, Ireland (87) : Ussher *et al.* 1908, Ussher 1910, Scharff, Seymour & Newton 1918, Barrett-Hamilton & Hinton 1910–21, Jackson 1929b, Coleman 1965, BM(NH).

Castletownroche Cave, Co. Cork (88) : Coleman 1965.

After the compilation of the above list we have been informed by Mr J. Carreck (*in litt.*) that he has also determined remains of *Lemmus lemmus* from deposits of Ipswichian (Zone IIb) age at Wretton, Norfolk (not marked on Fig. 1).

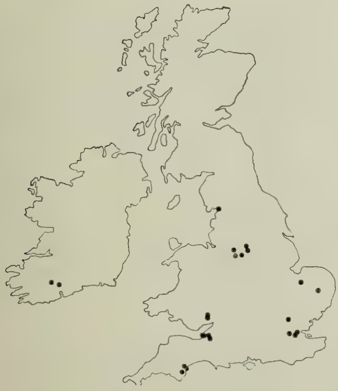


FIG. 13. Distribution of fossil remains of *Lemmus lemmus* (Linn.) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *L. lemmus* is distributed in Pleistocene sediments of England and southern Ireland. In many localities it has been found together with *Dicrostonyx torquatus*, but it is usually less numerous. Most of the fossil localities with *Lemmus* are of Last Glaciation age. Its occurrence at Nazeing, where it was found in peaty muds lying deeper than the calcareous muds in which

Dicrostonyx torquatus appears for the last time, seems to be the latest well-dated evidence of its presence in Britain. This may indicate that *Lemmus* disappeared slightly earlier than *Dicrostonyx,* though it could also be explained by lack of sufficient specimens.

Lemmus is known from at least four stages of the British Pleistocene. Earlier records are the lower middle Pleistocene site of Westbury-sub-Mendip, the Hoxnian of Hoxne and Swanscombe (Barnfield Pit, Upper Middle Gravel), and the stage or stages represented by the *Corbicula* Bed of Crayford and Erith and the Glutton Stratum of Tornewton Cave.

General distribution. The genus *Lemmus* has a circumpolar distribution ranging in the Old World from Scandinavia to the Bering Strait and including the arctic regions of North America. The differences between the Eurasiatic and American forms do not justify their distinction as different species (Sidorowicz 1964) : they can all be treated as subspecies of a single species, *L. lemmus*. *Lemmus* coexists in a great part of its range with *Dicrostonyx,* but is generally more southerly in distribution : it does not occur in Greenland or on the Canadian islands north of Viscount Melville Sound, where *Dicrostonyx* is abundant.

The genus *Lemmus* appeared very early in Europe. Its remains are known from middle Villafranchian deposits of Hungary, Poland and Germany. During the early Pleistocene it extended further south in eastern Europe than *Dicrostonyx,* and was present, for example, in Romania, where *Dicrostonyx* never penetrated. Its remains have been found at most early and middle Pleistocene fossil localities of central and western Europe and the genus is a characteristic element of the arctic fauna of the last two glaciations.

Systematic remarks. Fossil remains of *Lemmus* from the late Pleistocene of the British Isles and from the continent of Europe are indistinguishable, on the basis of teeth and preserved skeletal remains, from those of Recent *L. lemmus*. Villafranchian to middle Pleistocene remains are specifically different from the Recent form.

Genus ***CLETHRIONOMYS*** Tilesius 1850

Clethrionomys glareolus (Schreber 1780)

Bank vole

1846	*Arvicola pratensis* ; Owen : 208, fig. 78.
1870a	*Arvicola glareolus* (= *pratensis*) ; Sanford : 56.
1870b	*Arvicola glareolus* (Schreber) = *pratensis* (Baillon) = *riparia* (Yarrell) ; Sanford : 124.
1882a	*Arvicola* (*Evotomys* Coues & Allen) *glareolus* Schreber ; Newton : 82–83, pl. xiv, fig. 1–1c.
1900	*Microtus* (*Evotomys*) *glareolus* Schreb. ; Hinton, Kennard & Newton : 347–349.
1901	*Microtus glareolus* ; Hinton : 142.
1910b	*Evotomys* sp. ; Hinton : 492, 494, 497.
1926	*Evotomys harrisoni* Hinton : 216–217, pl. vii, fig. 2.
1926	*Evotomys kennardi* Hinton : 225–226, pl. vii, fig. 3.
1950	*Clethrionomys* sp. ; Schreuder : 629, 634–635.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Blackmore & Alston 1874, Newton 1882a, 1891, Hinton 1910b, Osborn 1922, Hinton 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop 1974.

Clacton, Essex (43) : Singer *et al.* 1973.

Hitchin, Hertfordshire (39) : Carreck 1959.

Swanscombe (Barnfield Pit, Upper Middle Gravels and Ingress Vale), Kent (30) : Stopes 1904, Hinton 1926b, Schreuder 1950, Sutcliffe 1964, Carreck (*in litt.*).

Aveley, Essex (34) : BM(NH).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1901, 1910b, 1926b, BM(NH).

Northfleet, Kent (29) : det. A. J. Stuart (*in litt.*).

Hutton Cave, Somerset (10) : Sanford 1870a, b, Blackmore & Alston 1874.

Tornewton Cave (Glutton Stratum and Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).

Alveston Fissure, Gloucestershire (15) : det. G. B. Corbet.

Bacon Hole, Glamorganshire (16) : Stuart (*in litt.*).

Kirkdale Cave, Yorkshire (77) : BM(NH).

Swanton Morley, Norfolk (66) : Stuart 1974.

West Wittering, Sussex (24) : BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Brixham Cave, Devon (4) : Lydekker 1885, Hinton 1926b, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Great Doward Cave, Herefordshire (17) : BM(NH).

Gwaenysgor Cave, Flintshire (68) : Jackson 1947.

Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910b, 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern, Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885, Kennard 1945–46, BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913.

Merlin's Cave, Herefordshire (18) : Hinton 1925.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Rowberrow Cavern, Somerset (11) : BM(NH).

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Happaway Cave, Devon (5) : BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Joint Mitnor Cave (layer X, Holocene), Devon (1) : BM(NH).

DISTRIBUTION IN THE BRITISH ISLES. The bank vole appeared in England for the first time during the Cromerian Interglacial. It was also present during the Hoxnian (Hitchin, Swanscombe). Although a few remains were found in the pre-hippopotamus Glutton Stratum of Tornewton Cave, this species is lacking from typical faunal assemblages of this time, for example from Clevedon Cave. It is a common element in deposits of Last Interglacial, Last Glaciation and Holocene age.

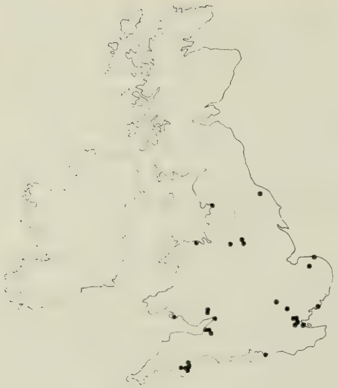


Fig. 14. Distribution of fossil remains of *Clethrionomys glareolus* (Schreber) in the British Isles.

Clethrionomys glareolus is an element of the forest fauna. It was probably not present in this country during the maxima of the glaciations, though it was able to reach it very early after the retreat of the ice and invaded the British Isles many times in all the interglacials and in post-glacial time.

General distribution. *C. glareolus* is now distributed throughout Europe, northern and central Asia and probably North America. Remains of the genus *Clethrionomys* are common in faunas of early middle Pleistocene age from continental Europe and have been described under different specific names, though they probably all belong to *C. glareolus*. *C. glareolus* is abundant in the interglacial and interstadial deposits of the late Pleistocene of Europe.

Systematic remarks. Only a few remains of *Clethrionomys* are known from the Norfolk Forest Bed. Although they were determined by Hinton (1926b) as '*Evotomys* sp.', they cannot be distinguished from Recent *C. glareolus*. The bank vole is a primitive, and very conservative, species of vole and its existence in Europe in the early Pleistocene is not unexpected.

Hinton (1926b) described from the Ightham Fissures two new species of *Clethrionomys*, '*Evotomys kennardi*' and '*E. harrisoni*', both from the same faunal assemblage. The material from Ightham is however a mixture of late Glacial and Recent bones and the holotype of *E. harrisoni* is a well-preserved skull of a typical *C. glareolus*. It is the skull of a young individual and its supposed characters (small dimensions, broad inter-orbital region) are related to its juvenile condition; it is probably a Recent specimen. '*E. kennardi*' seems to be of earlier geological age and its dimensions are somewhat larger than those of Recent specimens. According to Hinton (1926b), it belongs to the '*E. nageri*' group. *C. g. nageri* is now generally recognized as an Alpine subspecies (or perhaps only an ecotype) of *C. glareolus*, living under a more severe climate. It seems probable that during the difficult conditions of the Last Glaciation individuals of *Clethrionomys* grew bigger than during interglacial and postglacial times, but there are no reasons to determine them as a new species.

Genus ***PLIOMYS*** Méhely 1914

Pliomys episcopalis Méhely 1914

Vole, extinct

1914 ** *Pliomys episcopalis* Méhely : 195–203, pls 4–5.
1974 *Pliomys episcopalis* Méhely ; Bishop : 309, 314.

LOCALITY : Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974, 1975.

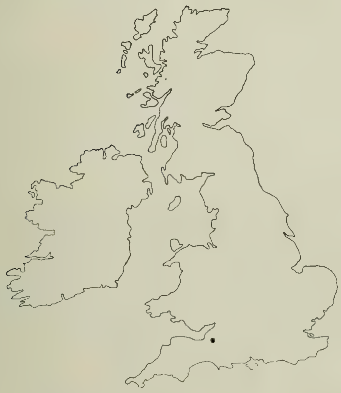


FIG. 15. Distribution of remains of *Pliomys episcopalis* Méhely in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *Pliomys* is known from only one British locality, Westbury-sub-Mendip, where it occurs in association with a lower middle Pleistocene fauna.

GENERAL DISTRIBUTION. *P. episcopalis* (type locality Betfia in Romania) appeared in the late Villafranchian of Europe and became widespread in the lower middle Pleistocene. In Italy it probably survived until the Holsteinian. Its remains are distributed from the European part of the Soviet Union to France and Italy. This species is generally recognized as an element of the steppe fauna.

Genus ***MIMOMYS*** Major 1902

Mimomys pliocaenicus Major 1902

Vole, extinct

1874 *Arvicola amphibius* (Linn.) ; Blackmore & Alston : 462–464 (*partim*).
1882a *Arvicola* (*Evotomys*) *intermedius* Newton : 83, pl. 13 (*partim*).
1902 *Mimomys pliocaenicus* Major : 102–107, figs 13–15.

DISTRIBUTION IN THE BRITISH ISLES. Although one rolled microtine tooth from the Red Crag has provisionally been referred to *Mimomys* by Spencer (1964) no remains identifiable at specific level are known from Britain earlier than the Norwich Crag. *M. pliocaenicus* has been found in the Norwich Crag and Weybourne Crag

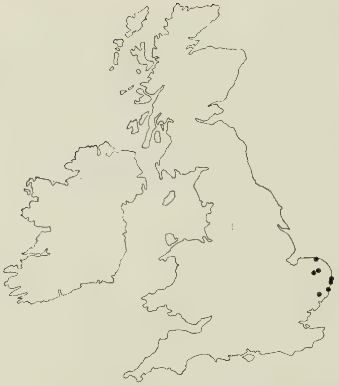


Fig. 16. Distribution of remains of *Mimomys pliocaenicus* Major in the British Isles.

of Covehithe, Easton Bavents and Sizewell, Suffolk, and Thorpe[1] and Bramerton, Norfolk (51, 50, 49, 48, 55). Its remains are also known from deposits of uncertain age at Kyson, Suffolk (47), and from the Weybourne Crag and probably Pastonian Forest Bed deposits at East Runton, Norfolk (64). All the specimens from this last locality seen by us in the British Museum (Natural History) are rounded, with visible traces of transport by water.

Bibliography. Blackmore & Alston 1874, Newton 1882a, Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Cranbrook 1955a, b, Carreck 1966, West 1968. Specimens have been seen in the BM(NH) and Ipswich Museum.

General distribution. *M. pliocaenicus* was first described by C. I. F. Major from the Val d'Arno in Italy. It is known from Late Villafranchian (Tiglian) deposits in France, Holland, Belgium, Germany, Poland, Hungary, Czechoslovakia, Romania and the Soviet Union (including Siberia). It has not been found in Cromerian (s.l.) faunal assemblages outside Britain, where it is of Pastonian age.

Systematic remarks. *M. pliocaenicus* is a characteristic species. It developed from smaller and more primitive ancestors living in the early Villafranchian (*M. polonicus* Kowalski) and disappeared or rather evolved into other species at the end of the Tiglian Interglacial.

[1] There are several places in East Anglia known as Thorpe and the location of the *M. pliocaenicus* site is not proved beyond doubt. The two most likely localities are Thorpe near Norwich, Norfolk, and Thorpe near Aldeburgh, Suffolk. C. I. F. Major (1902) described specimens collected by Mr Fitch from Thorpe, preserved in the Norwich Museum, though he did not indicate the county in which the Thorpe in question is situated. Carreck (1966) assumed that it was the Thorpe near Aldeburgh. Mr Fitch is known to have collected in the Norwich Crag of the Norwich area, however, and as the specimens subsequently found their way to Norwich Museum the possibility that they came from the Thorpe near Norwich must also be considered. Mr H. E. P. Spencer (*in litt.*) favours the last-mentioned locality, since there is a well-documented Crag mammal site there, whereas he points out that Thorpeness in Suffolk is on Coralline Crag. Mr P. Cambridge informs us of a Norwich Crag pit at Shell Cottages, Thorpe, Aldringham, near Aldeburgh, Suffolk. He too thinks the Thorpe near Norwich, where there were formerly several Norwich Crag pits with mammalian remains, is the most likely locality for the remains of *M. pliocaenicus* described by Major. We have tentatively accepted the Norfolk alternative, and this is marked on Fig. 1 as locality 48.

Mimomys reidi Hinton 1910

Vole, extinct

1882a *Arvicola (Evotomys) intermedius* Newton : 83 (*partim*).
1910b *Mimomys reidi* Hinton : 491.

DISTRIBUTION IN THE BRITISH ISLES. This species is known in Britain from the Weybourne Crag at *Trimingham (61) and from the Norwich Crag at Sizewell (49). In the collections of the British Museum (Natural History) there are specimens from the Savin collection labelled 'West Runton, Upper Freshwater Bed', but they are probably mislabelled or were found in a secondary layer. Hinton (1926b) stated that this species was not found outside the Norwich and Weybourne Crags.

BIBLIOGRAPHY. Newton 1882a, Barrett-Hamilton & Hinton 1910–21, Hinton 1910b, 1926b. Specimens have been seen at the BM(NH) and Ipswich Museum.

GENERAL DISTRIBUTION. *M. reidi* (probably identical with *M. petenyi* Méhely 1914) is known from many localities of Tiglian age in Holland, France, Germany, Italy, Poland, Czechoslovakia, Hungary and the Soviet Union (including Siberia).

SYSTEMATIC REMARKS. The holotype of this species was described from the Weybourne Crag at Trimingham, Norfolk, but the systematic position of the remains determined as *M. reidi* from continental Europe presents a problem : different forms, probably different stages of the same phyletic line, appear to be represented.

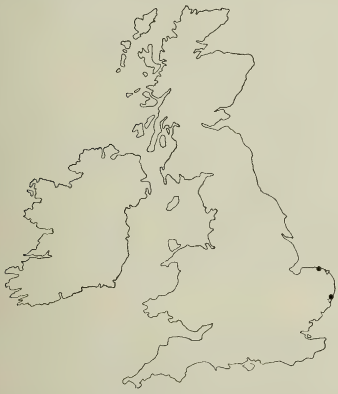


FIG. 17. Distribution of remains of *Mimomys reidi* Hinton (▽) and *M. newtoni* Major (●) in the British Isles.

Mimomys newtoni Major 1902

Vole, extinct

1902 *Mimomys newtoni* Major : 102–107, figs 13–15.

DISTRIBUTION IN THE BRITISH ISLES. In Britain *M. newtoni* is known from deposits ranging in age from Norwich Crag to either Weybourne Crag or Forest Bed. The holotype was described by Major (1902 : text-fig. 13, no. 7) as having been found in the 'East Runton Forest Bed'. It is now known that the deposits at East Runton are Pastonian and the holotype is most likely to be of this age. *M. newtoni* is also known from specimens in the British Museum (Natural History) collected by the Earl of Cranbrook from the Norwich Crag of Easton Bavents, Suffolk (50). The specimen in the BM(NH) from the Norwich Crag at Bramerton, Norfolk, (Hinton 1926b : 376, footnote) 'which may be referred to *M. newtoni*' is clearly different from the holotype and probably does not belong to the same species.

BIBLIOGRAPHY. Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b.

GENERAL DISTRIBUTION. *M. newtoni* is known outside Britain from deposits of Tiglian age in Holland, France, Germany, Poland, Czechoslovakia, Hungary and the Soviet Union.

SYSTEMATIC REMARKS. Small representatives of the genus *Mimomys* Major are so rare in the Lower Pleistocene strata of East Anglia that it is difficult to decide how many species are represented. Some of the specimens of '*M. newtoni*' from East Runton (M6967, numbers 19, 20 and 23) are visibly larger than the holotype (M_1 2·9 and 3·0 mm long, compared with 2·5 mm) and have cement in the re-entrant angles, absent in the type specimen. There may be two 'chronospecies' of different geological ages. The continental specimens (e.g. from Kadzielnia, Poland) are identical with these larger specimens of '*M. newtoni*' and different from the holotype. Further research will be necessary to determine whether an additional species should be established.

Mimomys savini Hinton 1910

Vole, extinct

1874	*Arvicola amphibius* (Linn.) ; Blackmore & Alston : 462–464 (*partim*).
1881	*Arvicola* (*Evotomys*, Coues) *intermedia* Newton : 258.
1902	*Mimomys intermedius* (Newt.) ; Major : 102–107.
1910b	*Mimomys savini* Hinton : 491.
1910b	*Mimomys majori* Hinton : 491.
1958	*Mimomys milleri* Kretzoi : 55.

DISTRIBUTION IN THE BRITISH ISLES. *M. savini* is a common species in the Upper Freshwater Bed at West Runton (65) and it is also known from East Runton (64). According to Newton (1882a), it has also been found at Cromer (63), Geldeston (53) and Kessingland (52). *Mimomys* cf. *savini* was recorded by Stuart (1974) from Cromerian deposits at Sugworth, near Oxford (21).

BIBLIOGRAPHY. Blackmore & Alston 1874, Newton 1881, 1882a, 1891, Reid 1890, Major 1902, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1920, 1926b, Kretzoi 1958, 1965, Pasquier 1972.

GENERAL DISTRIBUTION. *Mimomys savini* is widely distributed at localities of 'Cromerian' age in Holland, France, Germany, Italy, Poland, Czechoslovakia, Yugoslavia and the Soviet Union (including Siberia).

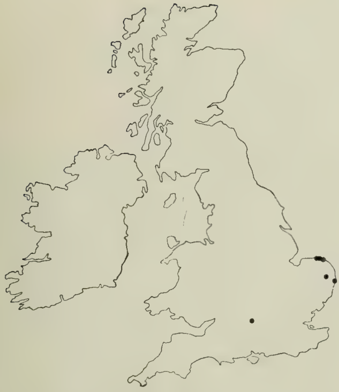


FIG. 18. Distribution of remains of *Mimomys savini* Hinton in the British Isles.

SYSTEMATIC REMARKS. *M. savini* was described by Newton (1881) from the Upper Freshwater Bed of *West Runton under the name of *Arvicola intermedia.* Hinton (1910b) described two further species of the same genus, *M. majori* and *M. savini*, from the same deposit. According to him, they differed from *M. intermedius* only in slight differences in the pattern of M_1, the dimensions of all the molars and the patterns of all other teeth being identical. Kretzoi (1958) found that *A. intermedia* is a junior homonym and must therefore be replaced by the name *Mimomys milleri* Kretzoi ; in a later paper (1965) he showed that the three species *M. intermedius, M. savini* and *M. majori* really represent only one variable species. The name of it must therefore be *Mimomys savini* Hinton, which is the oldest valid name. In fact all possible intermediate forms between typical *M. intermedius, M. savini* and *M. majori* are present in the abundant material from the Upper Freshwater Bed (Pasquier 1972). The presence of three species of one genus with identical dimensions in one and the same layer is also scarcely imaginable from the ecological point of view. Specimens determined as '*M. majori*' and '*M. savini*' have also been found in some Czechoslovak and German fossil localities, always associated with *M. intermedius.*

Genus *ARVICOLA* Lacépède 1799

The systematic study of even the living representatives of this genus presents many difficulties to zoologists. Miller (1912) divided living populations of water voles from western Europe into seven species but later investigators (for bibliography see Reichstein 1963) have demonstrated that nearly all the characters which were used for the diagnosis of these species lie within the limits of individual variation. Variations occur principally in the dimensions and in some proportions of the skull, proportions which may change allometrically with the changes of absolute dimensions.

Cytological studies support the view that there are only two living species in this genus, *A. sapidus* Miller 1908, from the south of France and the Iberian Peninsula, and *A. terrestris* (Linnaeus 1758) distributed throughout the rest of Europe as well as the northern part of Asia and the Middle East. The Recent population in Britain belongs to this last species. Reichstein (1963), after a very thorough analysis, found distinct but small craniological differences between the two species of *Arvicola* and further differences were reported by Corbet *et al.* (1970).

The systematic study of fossil forms, usually possible only from teeth and fragmentary skulls, is still more difficult. Remains from glacial deposits are usually larger than those from the interglacials and interstadials or from the Holocene, and most of the characters which have been used for creating new fossil species of water voles are expressions of individual variability, present also in Recent species. It seems beyond doubt that *Arvicola* developed from a late form of the genus *Mimomys*, most likely *Mimomys savini*, through the progressive reduction of the formation of roots in the molars and acquisition of the continual growth of these teeth. One character, typical of *Mimomys*, is nevertheless retained in geologically older populations of *Arvicola* : the enamel of the cheek-teeth is thinner on the concave and thicker on the convex sides of the salient angles, the reverse being true in the late Pleistocene and Recent populations. The two forms are united by a full series of intermediate specimens. O. Fejfar (in Koenigswald 1970) re-examined the holotype of *Mimomys cantianus* Hinton from the Hoxnian deposits of Ingress Vale, Swanscombe, and found that there is no trace of root-formation. This form must therefore be included in the genus *Arvicola*. *Arvicola cantiana* (Hinton) is the oldest available name for the primitive representatives of *Arvicola* and later names such as *A. bactonensis*, *A. greeni* and *A. praeceptor* must be treated as synonyms.

Koenigswald (1972, 1973) also studied the stratigraphical range of the various stages of the *Mimomys–Arvicola* lineage from European localities and defined a series of faunal groups :

(a) A *Mimomys savini* fauna, including the Upper Freshwater Bed of West Runton.
(b) and (c) *Arvicola* faunas groups 1 and 2, both with *A. cantiana* (Koenigswald included Swanscombe in group 2).
(d) *Arvicola* fauna group 3, with *A. terrestris*.

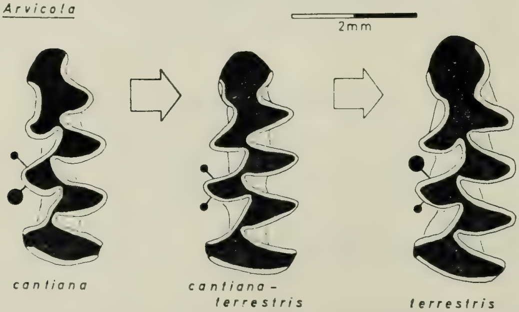


Fig. 19. Development of the enamel layer in Middle European forms of *Arvicola*. *Arvicola cantiana* (Elster–Riss) ; *Arvicola cantiana-terrestris* transition form (Riss–Eem) ; *Arvicola terrestris* (Eem–Holocene). From Koenigswald (1973 : 164).

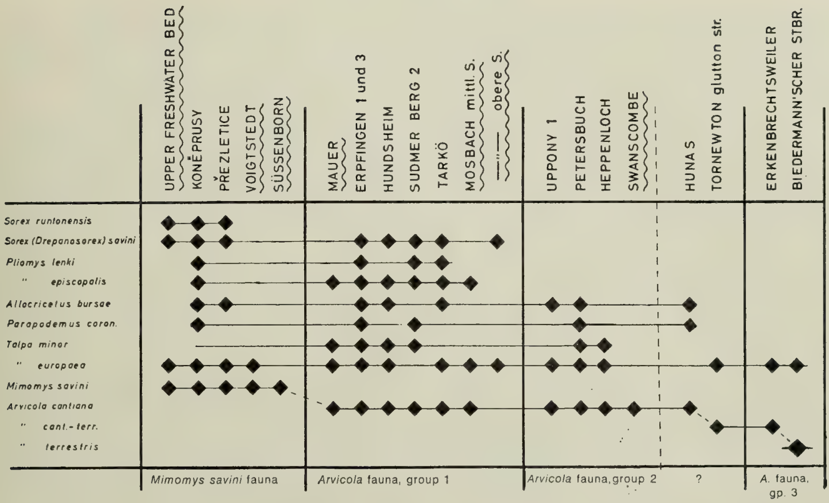


FIG. 20. Chronological distribution of *Arvicola* and other stratigraphically important small mammal species in European Pleistocene faunas. From Koenigswald (1973 : 161).

He referred the Glutton Stratum of Tornewton Cave to an intermediate stage between groups 2 and 3 (Fig. 20).

Koenigswald made a further study of British *Arvicola* remains in 1974 and (pers. comm.) assigned the phylogenetic position, between *A. cantiana* and *A. terrestris*, of the finds from various sites as follows :

A. cantiana ——→ intermediate forms ——→ *A. terrestris*

Clacton	Aveley	Barrington	Ightham
Swanscombe (Barnfield Pit and Ingress Vale)	Crayford	Joint Mitnor Cave	Kent's Cavern (Cave Earth)
	Grays	Swanton Morley	Wye Cave (= Merlin's Cave)
Ostend	Stutton	Tornewton Cave (Otter Stratum)	Tornewton Cave (Reindeer Stratum)
Westbury-sub-Mendip		Tornewton Cave (Glutton Stratum)	

These findings are of very far-reaching stratigraphical importance. *A. cantiana* appears for the first time in Britain at the 'late Cromerian' site of Westbury-sub-Mendip, which appears to represent Koenigswald's group 1, and is also present in the Hoxnian deposits of Clacton and Swanscombe. The transition form is represented by remains from the cold stage represented by the Glutton Stratum of

Tornewton Cave, in the Otter Stratum of that cave (where it is apparently slightly more advanced) and in the Last Interglacial hippopotamus faunas of Barrington, Joint Mitnor Cave and Swanton Morley. *A. terrestris* is characteristic of Last Glaciation and Holocene faunas.

It must be noted that Hinton's and Koenigswald's divisions between *A. cantiana* and *A. terrestris* do not exactly coincide. Koenigswald, from a re-examination of the specimens from the Barrington hippopotamus site, considered that the *Arvicola* remains from this locality should be attributed to the *A. cantiana-terrestris* transition form rather than to *A. praeceptor* (= *A. cantiana*), as determined by Hinton (1926b : 393). Stuart (see p. 69) has suggested that both forms are present. The specimens from the Last Interglacial site of Hessle, Yorkshire, attributed by Hinton (in Bisat 1940) to *A. praeceptor*, but which Boylan (1967) considered to lie within the normal range of variability of *A. terrestris*, have not been re-examined during the present investigation.

Surprisingly the remains from Aveley, Grays Thurrock, Harkstead and Stutton (currently widely regarded as Last Interglacial, though most if not all are sites without hippopotamus – the undoubted hippopotamus remains from Grays were collected more than a century ago and their exact provenance within the terrace complex of that area is unknown) are advanced *A. cantiana* and appear to be earlier than the pre-hippopotamus Glutton Stratum of Tornewton Cave.

The Crayford record of *A. cantiana* must be accepted with some reserve. Although *Arvicola* is recorded from this locality by Dawkins & Sanford (1866) and by Whitaker (1889) it was not mentioned by Hinton (1900a, b, 1910b, 1926b). The present determination is based on a single specimen in the British Museum (Natural History).

Arvicola cantiana (Hinton 1910)

Water vole, extinct

1846 *Arvicola amphibia* ; Owen : 201–205 (*partim*).
1882a *Arvicola amphibius* ? Linnaeus ; Newton : 87–88.
1902 *Microtus intermedius* ; Hinton & White : 414–415.
1910b *Mimomys cantianus* Hinton : 491.
1926b *Arvicola bactonensis* Hinton : 386–389.
1926b *Arvicola greeni* Hinton : 389–391, fig. 106, 1–2.
1926b *Arvicola praeceptor* Hinton : 391–394, fig. 106, 3–17.
1970 *Arvicola cantiana* (Hinton) ; Koenigswald : 418–420.

LOCALITIES : Ostend, Norfolk (57) : Owen 1846, Newton 1882a, Lydekker 1885, Hinton 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop 1974, 1975.

Clacton-on-Sea, Essex (43) : Hinton in Warren 1955, Sutcliffe 1964, BM(NH).

*Swanscombe (Ingress Vale and Barnfield Pit, Lower Loam), Kent (30) : Hinton & White 1902, Stopes 1904, Hinton 1910b, 1926b, Barrett-Hamilton & Hinton 1910–21, Sutcliffe 1964, Koenigswald 1970, BM(NH).

Aveley, Essex (34) : BM(NH).

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1910b, 1926b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Ilford, Essex (35) : Dawkins & Sanford 1866, Whitaker 1889, Newton 1890a, Johnson & White 1900, Hinton 1900a, b, 1910b, 1926b, BM(NH).

Stutton, Suffolk (44) : Stuart collection and seen in Ipswich Museum.

Harkstead, Suffolk (44) : Ipswich Museum – Stuart (*in litt.*).

Northfleet, Kent (29) : det. A. Stuart.

Crayford, Kent (27) : Dawkins & Sanford 1866, Whitaker 1889, BM(NH).

Arvicola cantiana-terrestris transition form

(see pp. 99–102 above)

LOCALITIES : Tornewton Cave (Glutton Stratum and Otter Stratum), Devon (3) : Kowalski 1967, (BM(NH).

Barrington, Cambridgeshire (40) : Hinton 1926b (but see note on p. 69), BM(NH).

Joint Mitnor Cave (layer IV), Devon (1) : BM(NH).

Minchin Hole, Glamorganshire (16) : det. A. J. Stuart.

Stoke Tunnel Beds, Suffolk (46) : Ipswich Museum.

Swanton Morley, Norfolk (66) : Stuart, pers. comm.

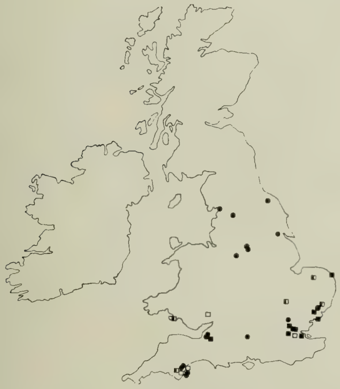


FIG. 21. Distribution of fossil remains of *Arvicola cantiana* (Hinton) (■) and *A. terrestris* (Linn.) (□) in the British Isles. (Transition form ◧, not studied ●.)

Arvicola terrestris (Linnaeus 1758)

Water vole

1846	*Arvicola amphibia* ; Owen : 201–205 (*partim*).
1847	*Hypudaeus spelaeus* Cuv. ; Giebel : 88.
1872	*Arvicola amphibius* Desm. ; Dawkins & Sanford : 180.
1910a	*Arvicola abbotti* Hinton : 34–35.
1960	*Arvicola amphibius terrestris* Bramwell : [10].

Localities : Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Kent's Cavern (Cave Earth), Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885, Hinton 1926b, Kennard 1945–46, Carreck 1957, BM(NH).

Tornewton Cave (Reindeer Stratum), Devon (3) : Kowalski 1967.

Wye (= Merlin's) Cave, Herefordshire (18) : Bate 1901, Hinton 1926b, BM(NH).

Arvicola cantiana / A. terrestris complex

(phylogenetic position not studied)

With the exception of Hoxne (Hoxnian) and Bacon Hole, Hessle, Kirkdale Cave and the Hyaena Stratum of Tornewton Cave (which are Last Interglacial) the following sites are all believed to be of Last Glaciation or Holocene age. The *Arvicola* remains are probably mostly advanced forms.

Localities : Hoxne, Suffolk (54) : Wolff (*in litt.*).

Bacon Hole (16) : Stuart (*in litt.*).

Bobbitshole, Suffolk (46) : Ipswich Museum, det. J. N. Carreck.

Hessle, Yorkshire (74) : Lamplugh 1891, Bisat 1940, Catt & Penny 1966, Boylan 1967, specimen in Institute of Geological Sciences Museum, London, not seen by K. K.

Kirkdale Cave, Yorkshire (77) : Owen 1846, Giebel 1847, Dawkins & Sanford 1866, Lydekker 1885, Hinton 1926b, BM(NH).

Tornewton Cave (Hyaena Stratum), Devon (3) : Kowalski 1967.

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, 1926b, BM(NH).

Brixham Cave, Devon (4) : Hinton 1926b, Carreck 1957, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, 1912, Hinton 1926b, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Gough's Cave, Somerset (12) : BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913, BM(NH).

Levaton Cave (2) : Carreck 1957.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Happaway Cave, Devon (5) : Hinton 1926b, Carreck 1957, BM(NH).

Nazeing, Essex (37) : Hinton 1952, BM(NH).

Cowside Cave No. 3, Yorkshire (78) : BM(NH).

Thatcham, Berkshire (Holocene, 23) : Wymer 1962.

General distribution of *Arvicola*, and systematic remarks. As stated above, the forms described as *A. greeni*, *A. bactonensis* and *A. praeceptor* must be treated as synonyms of *A. cantiana*. The first two of the above-mentioned species were described by Hinton (1926b) from specimens collected at Ostend, near Bacton, Norfolk, during the first part of the nineteenth century. *A. bactonensis* is known only from the holotype and *A. greeni* is represented only by two isolated teeth. The stratigraphic position of these remains is uncertain. Hinton (1926b) suggested that they were contemporary with the Cromer Forest Bed or only slightly younger. As *Arvicola* is not represented at the Cromerian type locality of West Runton, where the ancestral form *Mimomys savini* is present, it must be supposed that these specimens are from later deposits. They may be equivalent in age to the faunal assemblage of Westbury-sub-Mendip, where *A. cantiana* is present.

A. cantiana is known, under various names, from numerous localities of Holsteinian (Hoxnian) age in continental Europe and Siberia. Remains of *A. terrestris*, to which species it gave rise, are abundant from the Upper Pleistocene of Europe, including England and Wales. Like other voles, *Arvicola* never reached Ireland.

A. terrestris is now widely distributed in nearly all Europe and in cold and temperate parts of Asia, as far south as Persia and Palestine. It lives mostly near water, but under diverse climatic and vegetational conditions, ranging from the taiga belt, through deciduous forest and steppe, to the deserts in the south. As a species of high ecological tolerance it was present during the Pleistocene under both glacial and interglacial conditions.

Genus ***PITYMYS*** McMurtrie 1831

Many zoologists are of the opinion that *Pitymys* is only a subgenus of *Microtus*. *Pitymys* is morphologically similar to *Microtus*, *sensu stricto*, and is rather similar in its ecology, but the living forms are biologically quite different. Chaline (1972), who studied fossil vole remains from the French Pleistocene, came to the conclusion that fossil forms of *Pitymys* are nothing but morphotypes of *Allophaiomys pliocaenicus* Kormos 1932. If this is correct, then *A. pliocaenicus* would be a junior synonym of *Pitymys arvaloides* and its name must be changed accordingly. In his opinion the Recent subgenus *Pitymys* is polyphyletic and its members are more closely related to different forms of *Microtus* than to one another. In the opinion of one of us (K. K.) Chaline underestimates the ecological similarity of Recent species of *Pitymys* and all other zoological evidence, basing his conclusions on the pattern of M_1 only. For this reason he is unable to follow Chaline's suggestions.

Voles of the *Pitymys* group dominated the European vole faunule during the Cromerian Interglacial. They were still common during the Hoxnian, after which they disappeared completely from Britain. Their distribution in Europe and western Asia is now rather discontinuous. The first evidence of the presence of *Pitymys* in Britain was published by Major in 1902. Hinton (1923a) described two different species from the Upper Freshwater Bed of West Runton, *P. gregaloides* and *P. arvaloides*. They are clearly distinct species, though in continental Europe intermediate specimens are present. If *Pitymys* is only a subgenus of *Microtus*, a very prevalent opinion among Recent mammalogists, the name *Pitymys arvaloides* Hinton is a taxonomic homonym and must be replaced by a new name, *Microtus* (*Pitymys*) *arvalidens* Kretzoi 1958. In the opinion of K. K. it is more convenient to treat *Pitymys* as a separate genus and the name given by Hinton is therefore retained here.

Pitymys arvaloides Hinton 1923

Pine vole, extinct

1882a	*Arvicola arvalis* Pallas ; Newton : 88–89, pl. xiv, figs 2–5.
1902	*Microtus* (*Pitymys*) sp. ; Major : 107, fig. 15 (28).
1923a	*Pitymys arvaloides* Hinton : 541–542.
1958	*Microtius* (*Pitymys*) *arvalidens* Kretzoi : 57 (new name for *Pitymys arvaloides* Hinton 1923, non *Arvicola arvaloides* Pomel).
1972	*Allophaiomys pliocaenicus* Kormos ; Chaline : 104.

Localities : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1882a, Major 1902, Hinton 1923a, 1926b, Kretzoi 1958, Chaline 1972, BM(NH).

Hitchin, Hertfordshire (39) : Carreck 1959 : 326 (det. as *P.* cf. *arvaloides*).

Swanscombe (Barnfield Pit, Lower Gravel and Lower Loam), Kent (30) : Carreck 1959 (: 326), Sutcliffe 1964.

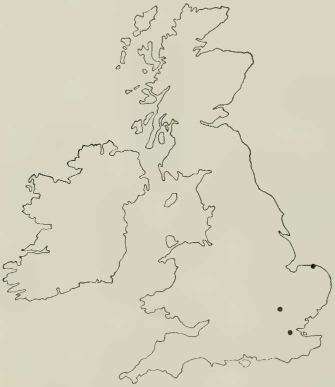


Fig. 22. Distribution of remains of *Pitymys arvaloides* Hinton in the British Isles.

Distribution in the British Isles. *P. arvaloides* is abundant in the Cromerian Upper Freshwater Bed at West Runton. It is present also in deposits of the lower part of the Hoxnian Interglacial, but disappears completely before its end. There is at present no evidence of its presence in Britain during the Anglian cold phase and it is probable that it invaded this country from the European continent twice.

General distribution and Systematic remarks. *P. arvaloides* is present at numerous localities of 'Cromerian' age on the continent (Italy, Yugoslavia, Germany, Hungary, Poland, Czechoslovakia, Austria, the European part of the Soviet Union and Georgia). Nearly everywhere it has been found together with *P. gregaloides*. It is not impossible that the two species, different in the morphology of M_1 but of identical dimensions, are only two forms of one polytypic species.

Pitymys gregaloides Hinton 1923

Pine vole, extinct

1882a	*Arvicola gregalis* Pallas ; Newton : 90–91, pl. xiv, figs 6, 6a.
1891	*Microtus* (*Arvicola*) *gregalis* Pallas ; Newton : 53.
1923a	*Pitymys gregaloides* Hinton : 541–542.
1972	*Allophaiomys pliocaenicus* Kormos ; Chaline : 104.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Newton 1882a, 1891, Hinton 1923a, 1926b, BM(NH).

Westbury-sub-Mendip Fissure, Somerset (13) : Bishop 1974, 1975.

Kent's Cavern, Devon (6) : Hinton 1926b, Kennard 1945–46, BM(NH).

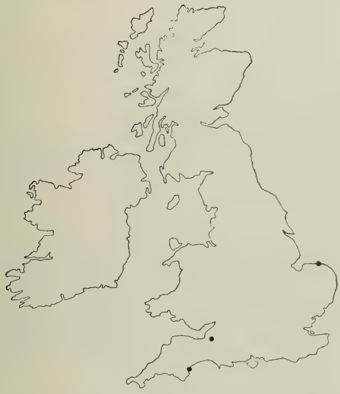


FIG. 23. Distribution of remains of *Pitymys gregaloides* Hinton in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *P. gregaloides* is present in Cromerian deposits at West Runton and at the Westbury Fissure, together with *P. arvaloides*. Two specimens, one preserved in the British Museum (Natural History), the other in Bristol Museum, are known from Kent's Cavern. The stratigraphical position of these specimens is unknown, but the species has not yet been recorded from any British Hoxnian locality and it is likely that they are of pre-Hoxnian age.

GENERAL DISTRIBUTION AND SYSTEMATIC REMARKS. *P. gregaloides* is present, together with *P. arvaloides*, at numerous localities in central and southern Europe dated as Cromerian (*sensu lato*).

Genus ***MICROTUS*** Schrank 1798

The genus *Microtus* now holds the dominant position in the subfamily Microtinae, being both most highly differentiated and most individually numerous. In the fossil state molar teeth make up most of the finds, mandibles occurring less commonly and complete skulls only in exceptional cases. Furthermore, it should not be forgotten that in living populations the variability of the molar pattern is sometimes enormous (Kowalski 1970) and this variability may be discontinuous, representing genetical polymorphism. At the same time there are species, clearly differentiated in external characters and in biological requirements, in which the teeth are nearly identical (e.g. the lower teeth of *M. agrestis* and *M. arvalis* cannot be clearly distinguished, nor can the upper teeth of *M. arvalis* and *M. oeconomus*). All these factors make the correct determination of fossil remains, including the material from Britain described below, very difficult.

The genus *Microtus* appeared rather late in the European Pleistocene, being found first in the Cromerian Interglacial when *Pitymys* was still numerically dominant. In the Hoxnian Interglacial both genera lived together but in later sediments in Britain *Pitymys* disappeared completely and on the European continent it now plays only a subordinate role.

Microtus arvalinus Hinton 1923

Vole, extinct

1902	*Microtus* sp., recalling *M. arvalis* ; Major : 107, fig. 15 (27).
1923a	*Microtus arvalinus* Hinton : 541–542.
1972	*Microtus* (*Microtus*) *arvalis* (Pallas) ; Chaline : 106.

LOCALITIES : West Runton (Upper Freshwater Bed), Norfolk (65) : Major 1902, Hinton 1923a, 1926b, BM(NH).

Westbury-sub-Mendip, Somerset (13) : Bishop (pers. comm.).

Swanscombe (Lower Loam and Upper Middle Gravel), Kent (30) : Schreuder 1950, Sutcliffe 1964, BM(NH).

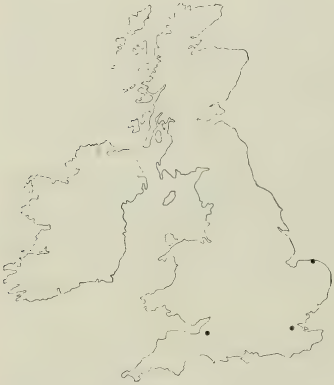


FIG. 24. Distribution of remains of *Microtus arvalinus* Hinton in the British Isles.

GENERAL DISTRIBUTION. *M. arvalinus* was present in Britain during the Cromerian and Hoxnian interglacials and the intervening Westbury stage. A small form of *Microtus*, with the M_1 pattern of the *M. arvalis/agrestis* group, is present in the Cromerian deposits of France, Germany, Austria, Czechoslovakia, Hungary, Romania and Yugoslavia.

Systematic remarks. *M. arvalinus* is identical in its M_1 pattern with Recent representatives of the *M. arvalis/agrestis* group, and differs from these only in its slightly smaller dimensions. It is probable that *M. arvalinus* is the ancestral form of *M. agrestis*. According to Chaline (1972), *M. arvalinus* is a synonym of *M. arvalis*, but there does not seem to be any good reason for putting it into this synonymy rather than that of *M. agrestis*.

Microtus agrestis (Linnaeus 1761)

Field vole

1846	*Arvicola agrestis* ; Owen : 206–207.
1847	*Hypudaeus bucklandii* Giebel : 88.
1894	*Microtus* (= *Arvicola*) *agrestis* ; Newton : 197.
1910b	*Microtus agrestis neglectus* ; Hinton : 494.
1910b	*Microtus agrestoides* Hinton : 493.
	Microtus arvalis and *Microtus arvalis/agrestis* group (*partim*) ; many authors.

General notes on the *Microtus arvalis/agrestis* group. During the nineteenth century most zoologists did not appreciate the differences between *M. arvalis* and *M. agrestis* and these two names must be regarded as synonyms in papers published at that time. Later on, the presence of the *M. arvalis* group on the Orkney Islands (*M. arvalis* does not survive today on the mainland of Britain and *M. agrestis* does not occur on Orkney) led to the hypothesis that *M. arvalis* was the first *Microtus* to reach Britain in the postglacial period. Under the influence of this hypothesis fossil remains of the *M. arvalis/agrestis* group were usually determined as '*M. arvalis*'. It must nevertheless be born in mind that only the upper M^2 provides diagnostic characters for distinguishing *M. agrestis* and *M. arvalis*. Both lower jaws and other isolated teeth are useless for this purpose (Dienske 1969). An example of the confusion which can occur in this context is provided by the *Microtus* remains from Dog Holes Cave, Lancashire. All the upper dentitions were correctly determined as '*M. agrestis*', but all the lower jaws were labelled '*M. corneri*' (= *M. arvalis*). This illustrates well the tendency to decide in each doubtful case in favour of *M. arvalis*.

In the site list for *M. agrestis* given below all the localities of *M. agrestis*, '*M. agrestoides*', '*M. arvalis/agrestis* group' and '*M. arvalis*' are enumerated.

Localities : Clacton-on-Sea, Essex (43) : Hinton 1923b, Singer *et al.* 1973.

Swanscombe (Upper Middle Gravels), Kent (30) : Schreuder 1950 (*M. arvalis/agrestis* group).

Ilford (Uphall Estate), Essex (35) : Hinton 1900a, b, Johnson & White 1900.

Grays Thurrock, Essex (33) : Hinton, Kennard & Newton 1900, Hinton 1901, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1924, 1926b, BM(NH) ('*M. agrestoides*').

Harkstead, Suffolk (44) : Ipswich Museum.

Stutton, Suffolk (44) : Ipswich Museum.

Northfleet, Kent (29) : Burchell 1935.

Tornewton Cave (Glutton Stratum, Hyaena Stratum, Reindeer Stratum, Diluvium), Devon (3) : Kowalski 1967, BM(NH).

Water Hall Farm Pit, Hertfordshire (38) : BM(NH).

Alveston Fissure, Gloucestershire (15) : det. G. B. Corbet.

Bacon Hole, Glamorganshire (16) : det. A. J. Stuart.

Bobbitshole, Suffolk (46) : Ipswich Museum, det. J. N. Carreck.

Barrington, Cambridgeshire (40) : BM(NH).

Joint Mitnor Cave, Devon (1) : BM(NH).

Kirkdale Cave, Yorkshire (77) : Owen 1846, Giebel 1847, Dawkins & Sanford 1866, Blackmore & Alston 1874, BM(NH).

Minchin Hole, Glamorganshire (16) : det. A. J. Stuart.

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Bleadon Cave, Somerset (10) : BM(NH).

Brixham Cave, Devon (4) : BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, 1912, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Gough's Cave, Somerset (12) : BM(NH).

Great Doward Cave, Herefordshire (17) : BM(NH).

Ightham Fissures, Kent (28) : Newton 1894, 1899b, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1921, 1926b, Jackson 1947, Zimmermann 1959.

Kent's Cavern, Devon (6) : Owen 1846, Dawkins & Sanford 1866, Blackmore & Alston 1874, Lydekker 1885–87, Kennard 1944–45, BM(NH).

King Arthur's Cave, Herefordshire (17) : BM(NH).

Langwith Cave, Derbyshire (72) : Mullins 1913, BM(NH).

Levaton Cave, Devon (2) : Carreck 1957.

Merlin's Cave, Herefordshire (18) : Hinton 1925.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Brean Down, Somerset (9) : Apsimon, Donovan & Taylor 1961.

Happaway Cave, Devon (5) : BM(NH).

Lynx Cave, Denbighshire (67) : Blore 1966.

Cowside Cave No. 3, Yorkshire (78) : BM(NH).

Corstorphine, nr. Edinburgh, Scotland (81) : Evans 1913.

Creag nan Uamh Cave, Inchnadamph, Scotland (83) : Peach & Horne 1917.

Distribution in the British Isles. *M. agrestis* is now widely distributed in Great Britain and many of the remains cited as fossils are probably of relatively recent age, in any case post-glacial.

The supposed earliest British occurrence of this group or species of rodents is at the Hoxnian locality of Swanscombe, where it is recorded as having been found in the Upper Middle Gravel in association with *M. arvalinus* (Schreuder 1950). The occurrence together of these two forms, which, it has been suggested (p. 109), are members of the same phylogenetic lineage, creates a problem. Schreuder

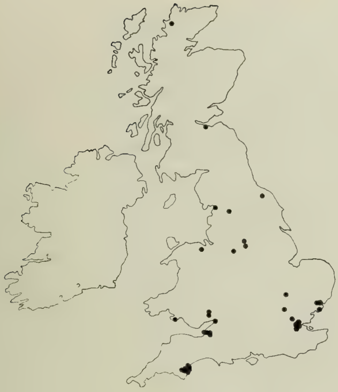


FIG. 25. Distribution of fossil remains of the *Microtus arvalis/agrestis* group in the British Isles.

distinguished the two forms at Swanscombe on grounds of size and stated that she would not have hesitated to accept as *M. arvalinus* the specimen determined by her as '*Microtus* sp., *arvalis/agrestis* group' had it not been so large. It has been pointed out by Corbet, however (pers. comm.), that there is great variation, which may reflect the age of the animal concerned, in the crown size of teeth of any microtine in which the teeth continue to grow during life. In view of the very small size of the sample studied by Schreuder, the occurrence of both *M. arvalinus* and *M. arvalis/agrestis* together in the same deposit is accepted here with some reserve. The remains are stratigraphically placed at about the time of transition between these two forms and a larger collection of remains is needed for study.

M. agrestis was common during the warm stages represented by both Grays Thurrock and Joint Mitnor Cave, and in the Glutton Stratum of Tornewton Cave, but is absent from the faunas of Crayford and Clevedon Cave. It was common during the Last Glaciation. At most localities where fossil remains have been found only lower jaws were present, but in each case where upper teeth were also found the second upper molar is of the typical *M. agrestis* pattern. There can be no doubt that the field vole was discontinuously present in Britain from at least the time of the Grays Thurrock deposits.

Hinton (1910b) created the name '*M. agrestoides*' for the specimens of *M. agrestis* from Grays Thurrock. He was surely influenced here by the supposition that Grays Thurrock has a very ancient fauna. The only distinctive character of his new species is 'the constant development of a fourth outer angle in the last upper molar'. This 'fourth angle' is present in a great proportion of specimens of Recent *M. agrestis* and its presence is not sufficient for specific determination.

According to Jackson (1929b), a skull of a vole which he regarded as close to *M. arvalis* was found in Kilgreany Cave, Co. Waterford, Ireland. This is the only possible evidence that voles ever reached Ireland; it was a skull with all teeth missing. It was found in the 'Lower Stalagmite' together with *Dicrostonyx* and human remains; '. . . a close examination of the sockets suggests that the species is the continental field vole *Microtus arvalis* or a close ally, and not the common field vole (*M. agrestis*)' (Jackson 1929b : 147).

The specimen has recently been re-examined by Savage (1966), who noted that it is notably fresh and unaltered and who had no doubt that it should be referred to *M. agrestis*. He pointed out that occasional vole remains have been found in north-east Ireland in pellets dropped by passing owls. On the basis of existing evidence, it is unlikely that voles ever reached Ireland.

GENERAL DISTRIBUTION. *M. agrestis* is now widely distributed in Europe, as well as in the cold and temperate parts of Asia. In Europe it extends north to include the whole Scandinavian peninsula and Finland. Fossil remains are known in continental Europe beginning with the Riss (penultimate) Glaciation.

Microtus arvalis (Pallas 1779)

Common vole

1910a *Microtus corneri* Hinton : 35–36.
Microtus arvalis (*partim*) ; many authors.

DISTRIBUTION IN THE BRITISH ISLES. Hinton (in Barrett-Hamilton & Hinton 1910–21, **2** : 467) correctly stated that :

> 'On several occasions fossils from various British deposits of Late Pliocene and Pleistocene age have been determined as belonging to *M. arvalis* (e.g. from fissures near Bath, Somerset, by Blackmore and Alston, Proc. Zool. Soc., 1874, 468) ; but in most cases such records imply, because of the fragmentary nature of the material, on which they are based, nothing more than the presence of a "vole" with an arvaloid, i.e. a normal dentition.'

According to Hinton (*loc. cit.*) the cranial remains from the Ightham fissures are 'apparently identical' with *M. arvalis* ; this locality probably marks the date of the arrival of the species in Britain.

Hinton (1910a) described from the Ightham fissures a new species, *M. corneri*, very similar to the Orkney vole, *M. orcadensis*. We now know, however, that *M. orcadensis* is nothing other than an isolated population of *M. arvalis*, possibly developed within historic times.

M. corneri has been recorded from the following localities :

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924.

Brixham Cave, Devon (4) : BM(NH) (det. Hinton).

Dog Holes, Lancashire (79) : BM(NH) (det. Hinton).

Ightham Fissures, Kent (28) : Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1921, 1926b, Jackson 1929, Hinton 1952, Zimmermann 1959.

Langwith Cave, Derbyshire (72) : Hinton 1910a, Mullins 1913.

Levaton Cave, Devon (2) : Carreck 1957 ('*Microtus arvalis* group, cf. *corneri* Hinton').

The status of *M. arvalis*, including *M. corneri*, in the British Pleistocene requires extensive further study. Although known today on the Orkney Islands, *M. arvalis* does not occur on the British mainland. There is geological evidence that the Orkney Islands have never been connected to the mainland since the last glacial phase, when ice covered the British Isles as far south as Norfolk and South Wales, and the local population of *M. arvalis* [= *orcadensis*] must therefore be a recent introduction from the continent (Corbet 1961). In Europe, *M. arvalis* is typical of the zone of mild climate, being absent from the Scandinavian peninsula and from northern Denmark. Its distribution as well as ecological data make its presence in the British Isles in the early postglacial period extremely improbable. The majority of fossil records of '*M. corneri*' from Britain are of rather doubtful value. As mentioned above, lower jaws of *Microtus* (which are specifically undeterminable) from Dog Holes Cave have been identified as *M. corneri* whilst all the skulls belong, without exception, to *M. agrestis*. The skull from Brixham Cave determined as belonging to *M. corneri* is probably a specimen of *M. oeconomus*.

One of the most potentially important collections for the study of *M. arvalis* is that from Ightham Fissures, Kent, where many excellently preserved vole skulls were collected. It is evident, however, that remains of both Pleistocene (Last Glaciation) and Holocene age have been mixed together. In such circumstances it is possible that sometimes a single species is represented in the fossil material by two different subspecies or by two different populations of different dimensions. Among the *Microtus* material from this locality, besides the typical skulls of *M. gregalis* and *M. agrestis*, there are two groups of larger and smaller skulls. Some of them may belong to *M. oeconomus*, and the skull selected as the holotype of *M. corneri* probably belongs here. Other specimens could be young individuals of this species, or they may really belong to *M. arvalis*.

Recently two small further collections of rodents have been studied by Corbet (pers. comm.) which suggest that *M. arvalis* may indeed have been present in England during the Last Glaciation. These are from Marlow, Buckinghamshire (25, Treacher Collection), and Beckford, Worcestershire (19, Briggs and Coope Collection), all in the British Museum (Natural History). The Marlow remains were apparently predominantly *M. arvalis*. There was also one first lower molar of *M. oeconomus*. Corbet considers that the lack of any second upper molars of *M. agrestis*, and the occurrence of only one lower molar of *M. oeconomus* among the many first lower molars (the teeth which distinguish these last two closely related species from *M. arvalis*), suggest that *M. arvalis* is the principal species present. The age of the Marlow rodents is uncertain, but is likely to be Last Glaciation.

Corbet considers that the Beckford specimens, if all one species, must be *M. arvalis*. They could be a mixture of *M. agrestis* and *M. oeconomus*, but the absence of the diagnostic second upper molar of *M. agrestis* or the first lower molar of *M. oeconomus* makes this improbable. Beckford is of Last Glaciation age, with a cold insect-fauna and ^{14}C dates of 27 650 ± 250 (Birmingham 293) and 27 300 ± 500 years (Birmingham 595).

At the present state of our knowledge neither the status of *M. arvalis* in the British Pleistocene nor the systematic position of '*M. corneri*' is clear. Craniometric analysis of the whole collection of *Microtus* from Ightham would be of great value. If *M. arvalis* was present in the British Isles it was an invasion of short duration during one of the phases of the Last Glaciation.

Microtus nivaloides Major 1902

Vole, extinct

1902 *Microtus nivaloides* Major : 106, fig. 19.
1923a *Microtus nivalinus* Hinton : 541–542.

LOCALITY : West Runton (Upper Freshwater Bed), Norfolk (65) : Major 1902, Barrett-Hamilton & Hinton 1910–21, Hinton 1923a, 1926b.

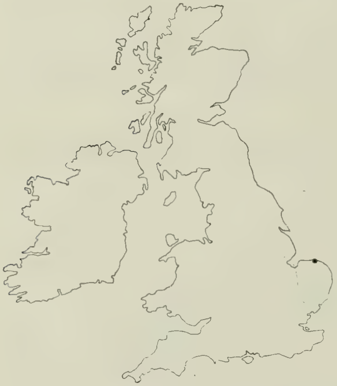


FIG. 26. Distribution of remains of *Microtus nivaloides* Major in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *M. nivaloides* is present in the Cromerian of Norfolk.

GENERAL DISTRIBUTION. Small representatives of the genus *Microtus* with the M_1 resembling that of *M. nivalis*, determined as *M. nivalinus* Hinton, *M. nivaloides* Major or *M. subnivalis* Pasa, have been recorded in 'Cromerian' deposits in Germany, Czechoslovakia, Hungary, Romania, Yugoslavia, Italy and the Ukraine.

SYSTEMATIC REMARKS. In addition to the well-defined form *M. nivaloides*, another from the same layer and locality was described as *M. nivalinus* by Hinton (1923a). Intermediate specimens between these two forms also occur and it is probable that only one species is represented. *M. nivaloides*, widely distributed in deposits of 'Cromerian' age in Europe, is probably the ancestor of *M. nivalis*, a common species in late Pleistocene localities. In Chaline's opinion (1972 : 151) *M. nivaloides* and *M. nivalinus* are synonyms of *M. nivalis*. This is in contradiction to the picture of evolution in the *M. nivalis* line as presented by the same author who considered that *M. nivalis* developed from *M. malei* not earlier than the penultimate glaciation.

Microtus nivalis (Martins 1842)

Snow vole

1907a *Microtus nivalis* (Martins) ; Hinton : 39–48 ; pl. 1, figs 5–23.
1907a *Microtus malei* Hinton : 49 ; pl. 1, figs 24–27.

Localities : Crayford and Erith (27) : Hinton 1907a, b, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, Chaline 1972, BM(NH).

Clevedon Cave, Somerset (14) : Hinton 1907a, b, 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Chaline 1972, BM(NH).

Cow Cave, Chudleigh (7) : det. G. B. Corbet.

Gough's Cave, Somerset (12) : BM(NH).

Tornewton Cave (Glutton Stratum), Devon (3) : Kowalski 1967, BM(NH).

Water Hall Farm Gravel Pit, Hertfordshire (38) : BM(NH).

East Wickham, Plumpstead, London : Hinton 1907b, 1926b, BM(NH).

Some additional records of *M. nivalis* exist in early papers. This species has been mentioned from a cave in the Forest of Dean, from Fisherton, Grays Thurrock and Swanscombe. Hinton (1926b) did not mention these localities in his monograph as containing *M. nivalis* and no remains of the snow vole have been seen by the writers among material collected from these sites.

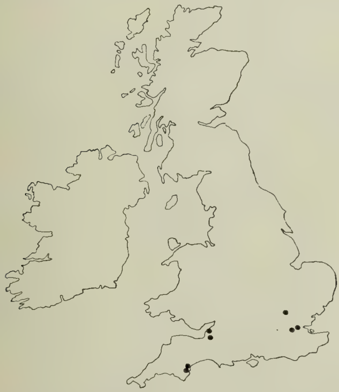


Fig. 27. Distribution of fossil remains of *Microtus nivalis* (Martins) in the British Isles.

Distribution in the British Isles. *M. nivalis* seems to be a typical element of the fauna of the period represented by Crayford and the Tornewton Cave Glutton Stratum. There was a stage when the genus *Microtus* was represented in the British Isles by two species only, *M. nivalis* and *M. oeconomus*. It is entirely absent from Devensian localities in Britain.

General distribution. *M. nivalis* is now distributed in mountain ranges, mostly in the Mediterranean area, from the Pyrenees in the west to Lebanon, the Caucasus and Kopet-Dag in the east. It inhabits treeless, mostly rocky or stony localities, not necessarily cold ones. During the Pleistocene it was more widely distributed.

Systematic remarks. *M. nivalis* has a very variable tooth-pattern. Its presence in Britain is beyond doubt, but the existence of a second species from this group, *M. malei*, does not seem probable. The teeth determined by Hinton (1907a) as belonging to *M. malei* were found exclusively in localities where *M. nivalis* is numerous, and all intermediate forms between typical *nivalis* and typical *malei* can be found. *M. malei* must therefore be taken as a synonym of *M. nivalis*. But according to Chaline (1972) *M. malei* is a valid species, and he designates as its lectotype the specimen M26481 in the British Museum (Natural History) from Clevedon Cave. In his opinion all the specimens from Clevedon Cave, determined by Hinton as belonging to *M. nivalis*, *M. malei* and *M. ratticeps*, represent only one variable species, *M. malei*. *M. nivalis* developed, according to Chaline, from *M. malei* during the late Pleistocene and was not present in Britain. His hypothesis, as stated above, seems to be contradictory, but it is possible that the representatives of the group of *M. nivalis* present in the lowland of Europe, including Britain, were different from the Recent *M. nivalis* from the European mountains. In such a case they must be named *Microtus malei* Hinton.

Microtus ratticepoides Hinton 1923

Vole, extinct

1923a *Microtus ratticepoides* Hinton : 541–542.

Localities : West Runton (Upper Freshwater Bed), Norfolk (65) : Hinton 1923a, 1926b, BM(NH).

Swanscombe (Lower Loam and Upper Middle Gravel), Kent (30) : Schreuder 1950, Sutcliffe 1964, BM(NH).

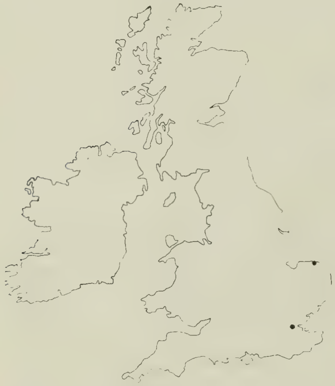


Fig. 28. Distribution of remains of *Microtus ratticepoides* Hinton in the British Isles.

Distribution in the British Isles. *M. ratticepoides* is known from deposits of Cromerian and Hoxnian age.

General distribution. *M. ratticepoides* has been recorded, mostly in 'Cromerian' faunal assemblages, in Holland, Germany, Romania, Czechoslovakia, Poland, Hungary and the European part of the Soviet Union including Georgia.

Systematic remarks. The tooth-pattern of *M. ratticepoides* is nearly identical to that of *M. oeconomus*, but the dimensions of the fossil form are slightly smaller than those of the Recent one. *M. ratticepoides* may be the ancestor of the Middle Pleistocene and Recent *M. oeconomus*.

Microtus oeconomus (Pallas 1776)
Root vole

1870b *Arvicola ratticeps* (Blasius) ; Sanford : 124–125, pl. viii, figs 1, 1a–1d.
1890a *Microtus* (*Arvicola*) *ratticeps* Key. and Bl. ; Newton : 453–456, figs 1–2.
1901 *Microtus ratticeps* ; Bate : 103–104.

LOCALITIES : Crayford and Erith (27) : Whitaker 1889, Newton 1890a, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Kennard 1944, Jackson 1947, Hinton 1952, BM(NH).

Harkstead, Suffolk (44) : Ipswich Museum.

Clevedon Cave, Somerset (14) : Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Tornewton Cave (Glutton Stratum, Reindeer Stratum, Diluvium), Devon (3) : Kowalski 1967, BM(NH).

Bacon Hole, Glamorganshire (16) : det. A. J. Stuart.

Water Hall Farm Pit, Hertfordshire (38) : BM(NH).

Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Bleadon Cave, Somerset (10) : Palmer 1934, BM(NH).

Chudleigh Fissure, Devon (7) : BM(NH).

Dog Holes Cave, Lancashire (79) : Jackson 1910, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Elder Bush Cave, Staffordshire (69) : Bramwell 1964.

Fisherton, Wiltshire (22) : Blackmore & Alston 1874, Bate 1901, Jackson 1910, Barrett-Hamilton & Hinton 1910–21, BM(NH).

Gough's Cave, Somerset (12) : BM(NH).

Great Doward Cave, Herefordshire (17) : BM(NH).

Ightham Fissures, Kent (28) : Newton 1894, Bate 1901, Jackson 1910, Hinton 1910b, Barrett-Hamilton & Hinton 1910–21, Hinton 1926b, Zimmermann 1959, BM(NH).

Isleworth, Middlesex (26) : BM(NH).

Kent's Cavern, Devon (6) : Sanford 1870b, Kennard 1945–46, BM(NH).

King Arthur's Cave, Herefordshire (17) : BM(NH).

Langwith Cave, Derbyshire (72) : Barrett-Hamilton & Hinton 1910–21, Mullins 1913.

Levaton Cave, Devon (2) : Carreck 1957.

Marlow, Buckinghamshire (25) : BM(NH).

Merlin's Cave, Herefordshire (18) : Hinton 1924.

Picken's Hole, Somerset (10) : Stuart 1974.

Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.

Dowel Cave, Derbyshire (71) : Bramwell 1960.

Etches' Cave, Derbyshire (71) : Pernetta 1966.

Lynx Cave, Denbighshire (67) : Blore 1966.
Nazeing, Essex (37) : Hinton 1952, BM(NH).
Cowside Cave No. 3, Yorkshire (78) : BM(NH).
Hay Wood Rockshelter, Somerset (10) : BM(NH).
Somerset levels, Huntspill Cut (8) : Hinton 1952.
Nornour, Isles of Scilly (91) : Pernetta & Handford 1970.
Creag nan Uamh Cave, Sutherland (83) : Peach & Horne 1917.

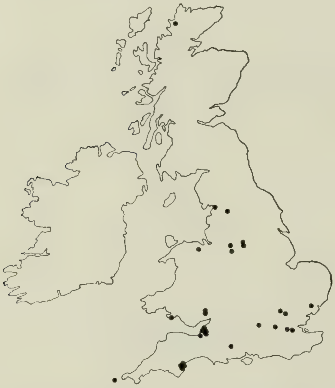


FIG. 29. Distribution of fossil remains of *Microtus oeconomus* (Pallas) in the British Isles.

DISTRIBUTION IN THE BRITISH ISLES. *M. oeconomus* is a widely distributed fossil species in England and Wales, which also reached northern Scotland. It is a dominant element of the Crayford fauna and is numerous in the sediments of the Last Glaciation. It was still present at the end of this period (Nazeing) and disappeared during postglacial times.

GENERAL DISTRIBUTION. *M. oeconomus* is now widely distributed in the northern parts of Europe, Asia and North America. In Europe its westernmost localities are in Holland and Germany and isolated colonies are known in Hungary and Austria. Fossil remains are common in the Late Pleistocene and Holocene layers of central Europe including France, Hungary and Switzerland.

SYSTEMATIC REMARKS. In Chaline's opinion (1972) *M. ratticepoides* is a synonym of *M. oeconomus*, which developed during the Last Glaciation, its ancestor being *M. malei*. This hypothesis is rather contradictory and lacks evidence, at least as far as material from the British Isles is concerned.

Microtus gregalis (Pallas 1779)

Narrow-skulled vole

1894	*Microtus* (= *Arvicola*) *gregalis* ; Newton : 197–198, pl. xi, fig. 12.
1910a	*Microtus anglicus* Hinton : 36–37.

LOCALITIES : Aveline's Hole, Somerset (11) : Davies 1921, Hinton 1921, 1924, BM(NH).

Bleadon Cave, Somerset (10) : BM(NH).
Brixham Cave, Devon (4) : BM(NH).
Chudleigh Fissure, Devon (7) : BM(NH).
Great Doward Cave, Herefordshire (17) : BM(NH).
Ightham Fissures, Kent (28) : Newton 1894, Hinton 1910a, b, Barrett-Hamilton & Hinton 1910–21, Hinton 1924, 1926b, 1952, Zimmermann 1959, Chaline 1972, BM(NH).
Isleworth, Middlesex (26) : BM(NH).
Kent's Cavern, Devon (6) : Kennard 1945–46, BM(NH).
King Arthur's Cave, Herefordshire (17) : BM(NH).
Langwith Cave, Derbyshire (72) : Hinton 1924, Mullins 1913.
Levaton Cave, Devon (2) : Carreck 1957 ('*Microtus* cf. *anglicus*').
Merlin's Cave, Herefordshire (18) : Hinton 1925.
Picken's Hole, Somerset (10) : Stuart 1974.
Pin Hole Cave, Derbyshire (73) : Jackson 1934, 1947.
Tornewton Cave (Reindeer Stratum), Devon (3) : Kowalski 1967, BM(NH).
Uphill Cave, Somerset (9) : Hinton 1926b.
Dowel Cave, Derbyshire (71) : Bramwell 1960.
Happaway Cave, Devon (5) : BM(NH).
Nazeing, Essex (37) : Hinton 1952, BM(NH).

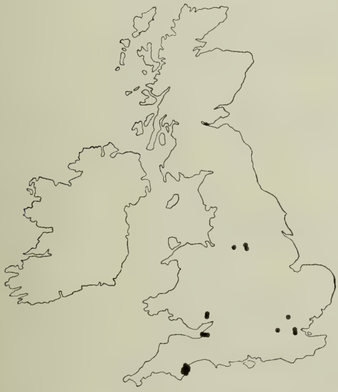


Fig. 30. Distribution of fossil remains of *Microtus gregalis* (Pallas) in the British Isles.

Although *M. anglicus* (= *M. gregalis*) is recorded from Dog Holes Cave (Jackson 1912) four specimens from this locality preserved in the British Museum (Natural History) and labelled by Hinton as *M. anglicus* do not belong to this species but to *M. agrestis*.

Distribution in the British Isles. *M. gregalis* was present in the southern parts of England during the Last Glaciation, but is absent in all earlier sediments. It probably reached Britain only once and disappeared before the end of the last glacial period.

General distribution. *M. gregalis*, the unique representative of the subgenus *Stenocranius* Kastschenko, is now distributed widely in northern and central Asia and in arctic Europe from the White Sea in the west to the Bering Strait in the east. In the western parts of its range it is associated with the tundra belt but in the east, where the climate is more continental, it is present also in the steppe and desert zone in eastern and central Asia.

In Europe it was common in the time of the Last Glaciation, reaching France and Britain in the west and Switzerland and Hungary in the south. According to Chaline (1972), it was present in France during both the last and penultimate glaciations.

Systematic remarks. *M. gregalis* was recorded in the Pleistocene of Europe by Nehring (1875 : 7). According to Hinton (1924), fossil remains from Europe are specifically distinct from *M. gregalis* and approach *M. tianschanicus* Büchner (now regarded as synonym of *M. eversmanni* Poljakov). In the modern systematics of this group *M. eversmanni* is recognized as a subspecies of *M. gregalis*. The morphology and dimensions of the European fossil specimens lie completely within the range of variability of the polytypic species *M. gregalis*. According to Chaline (1972) the name *anglicus* can be preserved to designate the subspecies of *M. gregalis* from the Last Glaciation localities of Europe.

Genus ***LAGURUS*** Gloger 1841

Lagurus lagurus (Pallas 1773)

Steppe lemming

1967 *Lagurus lagurus* (Pallas) ; Kowalski : 115–119, figs 1–24.

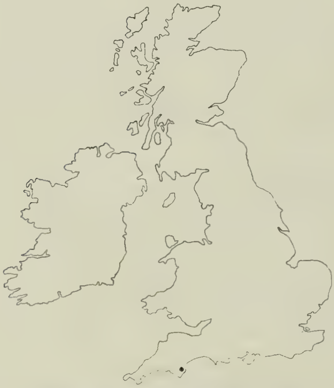


Fig. 31. Distribution of fossil remains of *Lagurus lagurus* (Pallas) in the British Isles.

Distribution in the British Isles. Remains of *Lagurus lagurus* have been found at only one locality, in the Glutton Stratum of Tornewton Cave, Devon (3) (Kowalski 1967). Sixty-three first lower molars (3·8 per cent of the total number of rodent remains in this layer) and many other teeth were found in this deposit, which dates from the cold stage preceding the interglacial hippopotamus-bearing Hyaena Stratum of this cave.

GENERAL DISTRIBUTION. *L. lagurus* developed during the Middle Pleistocene from more primitive forms of the genus *Lagurus*. It is now distributed in the steppe zone of Eurasia from the River Dnepr to Mongolia and Chinese Turkestan. Its fossil remains are relatively common in Upper Pleistocene localities in central and eastern Europe, but less so in western Europe. In France (Chaline 1973) it has been found in strata of the penultimate ('Riss') and early last (Würm) glaciations.

SYSTEMATIC REMARKS. The fossil British *Lagurus* remains are identical in dimensions and molar pattern with recent specimens of this species. The only character not observed in contemporary material is a tendency among the Tornewton specimens towards the fusion of the two anterior enamel triangles on the first lower molar (Kowalski 1967).

IV. HISTORY OF THE RODENT FAUNA OF THE BRITISH ISLES DURING THE PLEISTOCENE

In the earlier parts of this work rodent localities and rodent species were considered individually. In conclusion, let us attempt to construct from this information a generalized table of the rodent faunas of the various stages of the British Pleistocene. The construction of such a table must nevertheless be carried out with reserve. Rodent faunas were not uniform throughout the British Isles. Cold-adapted species in the north were able to coexist with more temperate species in the south, and during every glacial and interglacial stage there occurred a shifting of the vegetational zones which would have caused corresponding movements of the rodent populations.

Sometimes sea barriers prevented the movement of rodents. The known rodent faunas of the Lower Pleistocene and of the later glaciations of England are similar to those of the continent of Europe, suggesting land connections, whereas only a few rodent species are known from the later interglacials, suggesting separation. There is no evidence that any rodents crossed to Ireland until some stage during the Last Glaciation.

Fossil rodent material is seldom rich enough to demonstrate local or temporal differentiation within particular divisions of the Pleistocene of the British Isles and there are some stages, especially the earlier glaciations, from which no rodent remains are yet known. The incompleteness of the record of British rodents was strikingly demonstrated by the recent discovery of previously unrecognized rodent faunas in the Westbury Fissure and in Tornewton Cave. Further discoveries can be expected to provide an ever more detailed sequence for a long time to come.

The most likely stratigraphical relationship of the principal British rodent localities, at our present incomplete state of knowledge, and the known range of the various rodent species, is shown in Table 12. A series of faunal stages can be recognized. In ascending order these are as follows.

RED CRAG. The study of rodents from the earliest Pleistocene deposit of the British Isles, the Red Crag, is very difficult because of the mixing in this marine deposit of contemporary and derived fossils. *Castor fiber* is apparently a contemporary species. *Trogontherium minus,* known from Pliocene sediments on the continent of Europe, and *Hystrix* are apparently derived remains of pre-Pleistocene age.

ICENIAN CRAG AND PASTONIAN FOREST BED. The next faunal assemblage is that of the Icenian Crag and the earlier (Pastonian) part of the Forest Bed Series at East Runton. *Mimomys pliocaenicus* (from both deposits) and *M. reidi* (from the Icenian Crag) are species of great stratigraphic importance. On the continent of Europe they are limited to the Upper Villafranchian or Tiglian. There is no evidence of any difference between the British and European continental rodent faunas at this stage. *Trogontherium boisvilletti* and *Castor fiber* are two long-ranging rodents also present in both series of deposits.

CROMERIAN *sensu stricto.* The rodent fauna from the Cromerian type locality at West Runton is unusually rich, there being at least eleven species. *Trogontherium boisvilletti* and *Castor fiber* reappear. *Mimomys savini* replaces *M. pliocaenicus*; *Apodemus sylvaticus, Cricetus cricetus, Clethrionomys glareolus, Pitymys arvaloides, P. gregaloides, Microtus arvalinus, M. nivaloides* and *M. ratticepoides* make an appearance. *Sciurus whitei* occurs in the overlying marine 'Monkey Gravel'.

The West Runton fauna is predominantly of forest and meadow type, testifying to a mild climate, though *Cricetus cricetus* could point to colder or more continental conditions. No arctic elements are present. *Allophaiomys pliocaenicus* and lemmings, already present on the continent at the time of the earliest glaciations, are so far unrecorded from West Runton.

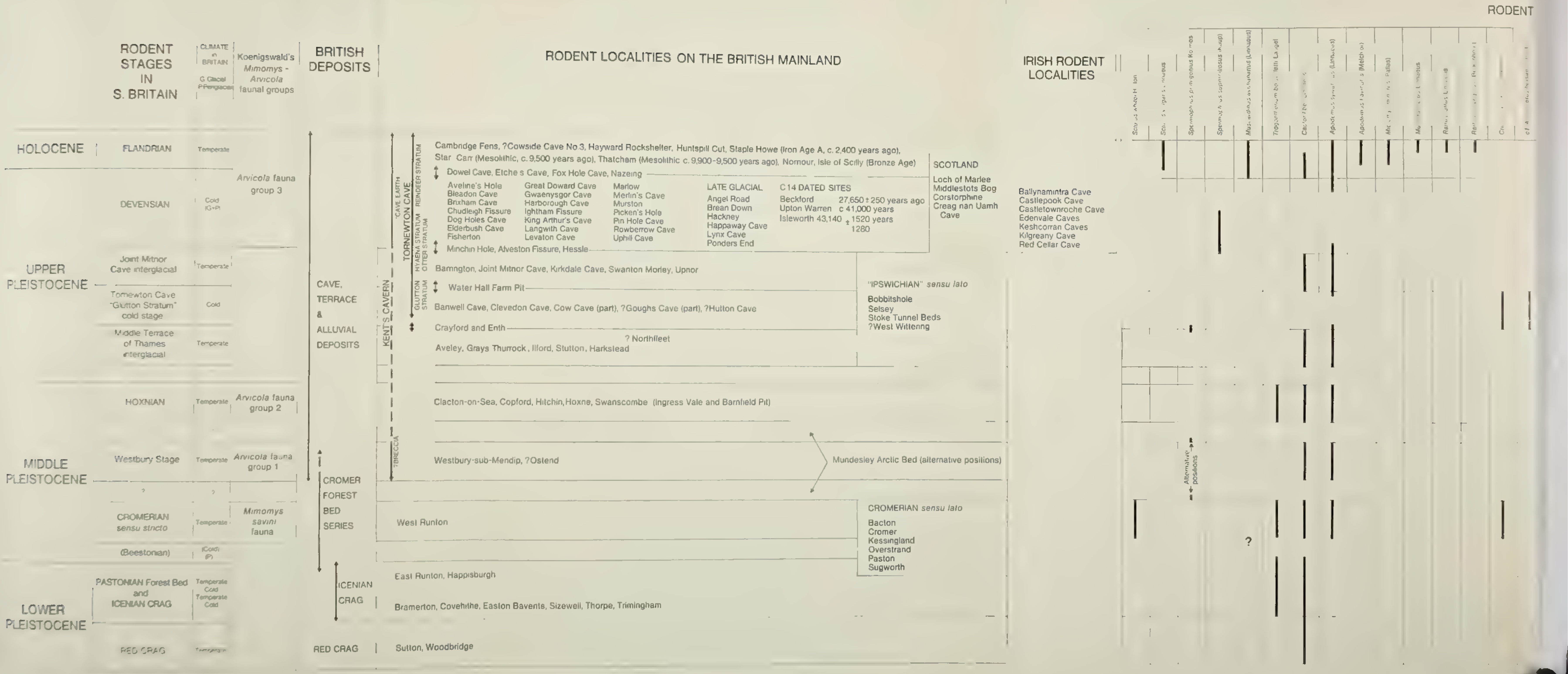
'WESTBURY STAGE'. The rich mammalian fauna from Westbury Fissure, described by Bishop (1974), does not at present fit into the generally accepted Pleistocene sequence of the British Isles. Bishop has presented evidence of a previously unrecognized stage later than the Cromerian *sensu stricto* of West Runton and possibly equivalent to Mosbach and other continental sites.

Although the richest rodent-bearing level at Westbury (the 'Rodent Earth') is the latest deposit in the fissure and may be slightly younger than the main bone deposit (the 'Calcareous Series') five rodent species are nevertheless represented in the latter. *Apodemus sylvaticus, Pitymys gregaloides* and *Microtus arvalinus* reappear; *Arvicola cantiana* and *Lemmus* sp. appear for the first time. All these forms persist into the 'Rodent Earth' which also contained *Dicrostonyx* sp., the earliest record in the British Pleistocene, and the only record from the British Pleistocene of *Pliomys episcopalis. Clethrionomys glareolus* reappears. Of special interest is the first appearance in the British Pleistocene of *Arvicola cantiana,* which apparently replaces *Mimomys savini,* believed to be an earlier stage in the same phylogenetic lineage, and which is so common at West Runton.

Castor fiber is represented in the lowest water-laid deposits of the cave. The lowest deposits of Kent's Cavern and the 'Forest Bed' deposit of Ostend, Norfolk, may also belong to this stage.

TABLE 12

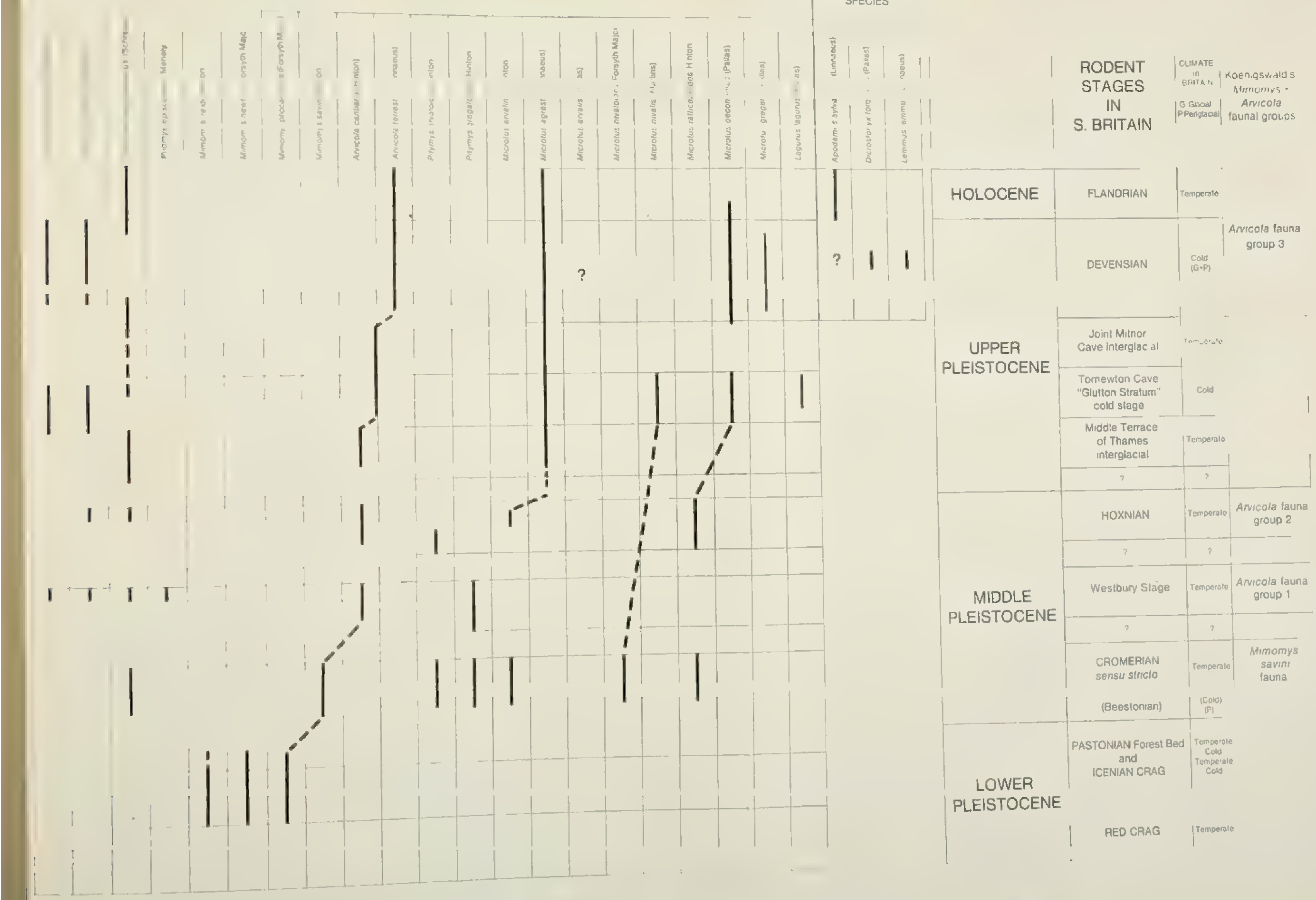
Probable chronological distribution of fossil rodent localities and rodent species from the British mainland and Ireland, according to ava



lable information

(*for* Hayward *read* Hay Wood)

SPECIES ON THE BRITISH MAINLAND



MUNDESLEY ARCTIC BED. The *Spermophilus* described by Newton (1882b) from a deposit with remains of arctic plants at Mundesley, Norfolk, provides the only known instance of a fossil rodent from a British Lower or Middle Pleistocene non-interglacial deposit. According to Newton the deposit was immediately overlain by thick glacial deposits which West & Wilson (1966) attributed to the Lowestoftian (Anglian) Glaciation. They referred underlying interglacial deposits to the Cromerian *sensu stricto*.

For the time being the exact relationship between the Mundesley Arctic Bed and the Westbury deposits must remain uncertain. If, as might be expected, Mundesley is later than Westbury then it is necessary to explain why the Westbury stage has not been recognized, except possibly at Ostend, in the Forest Bed sequence of East Anglia. If, on the other hand, it is earlier then it is necessary to postulate a hitherto unrecognized cold stage between the Cromerian *sensu stricto* and the 'Westbury' stage.

HOXNIAN DEPOSITS. The best sequence of deposits with rodent remains of Hoxnian age is that of Barnfield Pit, Swanscombe. A considerable time interval is believed to have occurred within this sequence, between the Lower Loam and the Middle Gravel (see p. 52). From the lowest deposit, the Lower Gravel, only *Pitymys arvaloides* has been recorded. In the overlying Lower Loam this species is accompanied by *Castor fiber, Arvicola cantiana, Microtus arvalinus* and *M. ratticepoides*.

These last two species continue into the Upper Middle Gravel, where they are joined by *Clethrionomys glareolus* and *Lemmus* sp. Although *Trogontherium boisvilletti* and *Apodemus sylvaticus* have not been recorded from Barnfield Pit, they are known from a nearby pit in the same terrace deposits at Ingress Vale. *Trogontherium boisvilletti* appears to have been common during the Hoxnian, being recorded also from Clacton, Copford and Hoxne. It is unknown from later deposits.

COMPARISON OF THE RODENT FAUNAS of West Runton, Westbury-sub-Mendip and Swanscombe. Although the geological evidence indicates at least one major glaciation between the time of accumulation of the deposits at West Runton and at Swanscombe, and although there are very great differences between the large mammals of the three sites mentioned above, changes in the rodent fauna were remarkably gradual. The distribution of the various rodent species is shown in Table 13.

Whilst incomplete collecting probably accounts for many of the gaps in the table a gradual replacement of species is nevertheless apparent. *Mimomys savini*, abundant at West Runton, appears to be replaced at Westbury by *Arvicola cantiana*. This species persists at Swanscombe and in slightly later deposits. *Microtus arvalinus* and *M. ratticepoides* are present at both West Runton and Swanscombe (the former occurs also at Westbury), but apparently disappear from the British Pleistocene after the Upper Middle Gravel. *Trogontherium boisvilletti* and *Pitymys arvaloides* are of similar distribution, last seen at Ingress Vale and in the Lower Loam of Barnfield Pit respectively. *Pitymys gregaloides* occurs at West Runton and Westbury but does not reappear at Swanscombe. *Microtus nivaloides* is not at present known from deposits later than West Runton. *Pliomys* is at present known

TABLE 13

Comparison of rodent species represented at West Runton, Westbury-sub-Mendip (Bishop 1974 and pers. comm.) and Swanscombe

	West Runton	Westbury-sub-Mendip			Swanscombe			
					Barnfield Pit			
	Upper Freshwater Bed	'Siliceous Group'	'Calcareous Group'	'Rodent Earth'	Lower Gravel	Lower Loam	Upper Middle Gravel	Ingress Vale
Sciurus whitei	×							
Trogontherium boisvilletti	×							×
Castor fiber	×	×				×		
Apodemus sylvaticus	×		×	×				×
Cricetus cricetus	×							
Dicrostonyx sp.				×				
Lemmus sp.			×	×			×	
Clethrionomys glareolus	×			×			×	
Pliomys episcopalis				×				
Mimomys savini	×							
Arvicola cantiana			×	×		×		×
Pitymys arvaloides	×				×	×		
P. gregaloides	×		×	×				
Microtus arvalinus	×		×	×		×	×	
M. nivaloides	×							
M. ratticepoides	×					×	×	

only from the youngest deposit at Westbury. *Dicrostonyx* and *Lemmus*, so common in British Upper Pleistocene deposits, appear for the first time at Westbury. *Lemmus* reappears in the Upper Middle Gravel of Swanscombe.

No major break is discernible in the above sequence of rodent faunas. The Westbury fauna has some characters in common with both West Runton and Swanscombe, confirming Bishop's supposition that it is of intermediate age. The rodent faunas of the three localities are similar to Koenigswald's *Mimomys savini* fauna, *Arvicola* fauna group 1 and *Arvicola* fauna group 2 of the continent of Europe (see p. 101) and suggest land connections during the periods concerned. A similarity of the large mammals of Swanscombe and those from the Holsteinian site of Steinheim an der Murr in Germany has previously been observed by Sutcliffe (1964).

NOTES ON THE WOLSTONIAN–IPSWICHIAN PART OF THE SUCCESSION. Although palaeobotanical evidence provides support for only one further interglacial in the

British Isles after the Hoxnian it is difficult to fit all the known Upper Pleistocene rodent faunas into such a simple sequence of events. The generally accepted Wolstonian–Ipswichian part of the succession appears, from the rodent and other evidence previously described, to be composite. The so-called 'Ipswichian' interglacial is here interpreted as double, with the Middle Terrace of the Thames representing a warm stage earlier than the Joint Mitnor Cave warm stage.

MIDDLE TERRACE OF THE THAMES INTERGLACIAL. Reasons for regarding the deposits of the Middle Terrace of the Thames (type locality Grays Thurrock) as representing the earlier of these two warm periods have been given on pp. 55–58. Ilford, Aveley, Harkstead, and Stutton in Suffolk are also included here. The known rodent fauna of this stage is very sparse. *Arvicola cantiana* reappears; other species include *Castor fiber*, *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*. Consideration needs to be given to the possibility that this stage is Hoxnian (Zeuner (1945) believed that Grays was of Penultimate Interglacial = Hoxnian age) but the occurrence of *Arvicola cantiana* in other Middle Terrace localities such as Aveley and Stutton, both of which have been claimed on palaeobotanical grounds to be Ipswichian, makes it unnecessary to resort to such an early date.

TORNEWTON CAVE GLUTTON STRATUM COLD STAGE. The *Arvicola* from the Glutton Stratum of Tornewton Cave is the transition form between *A. cantiana* and *A. terrestris*, suggesting that this deposit is later than the Middle Terrace of the Thames where the species is *A. cantiana*. We know that this stage was followed by a further interglacial, since these deposits were immediately overlain by the Hyaena Stratum, with remains of hippopotamus. Other species from the Glutton Stratum are *Microtus oeconomus* and *M. nivalis*, which make up the bulk of the rodent fauna, and also *M. agrestis*, *Lagurus lagurus* (the only British record of this species), cf. *Allocricetus bursae* and *Cricetus cricetus*. *Dicrostonyx torquatus* and *Lemmus lemmus* are present, but not abundant.

This assemblage closely resembles that of the Late Middle Terrace of Crayford and Erith, regarded by Hinton (1926b) as later than that of the Middle Terrace of Grays Thurrock. Rodents common to both Crayford and the Tornewton Cave Glutton Stratum are *Microtus oeconomus*, *M. nivalis*, *M. agrestis*, *Arvicola* sp., *Lemmus lemmus* and *Dicrostonyx torquatus*. Most of the species that are not common to both deposits are so rare in the British Pleistocene that stratigraphic comparison with other localities cannot be made. *Spermophilus primigenius* from Crayford and *Cricetus cricetus* from Tornewton Cave are unknown from any other post-Hoxnian British sites; cf. *Allocricetus bursae* (Tornewton Cave) is known from only one other British locality, Hutton Cave, which is of uncertain age. *Lagurus lagurus* is known only from Tornewton Cave.

The mollusc evidence suggests that the *Corbicula* Bed at Crayford, in which most of the rodent remains were found, is still interglacial, though absence of forest species of land mollusca indicates open grassland. The living representatives of the subgenus *Urocitellus*, to which *Spermophilus primigenius* belongs, are also open-country species. On the continent *S. primigenius* is unknown later than the 'penultimate' glaciation.

From the available evidence the most likely stratigraphic position for Crayford would seem to be the end of the Grays–Ilford–Aveley interglacial. *S. primigenius* prevents us from attributing a date late in the Pleistocene to the Crayford deposits. Crayford apparently heralds the arrival of the Tornewton Cave Glutton Stratum rodent fauna and marks the beginning of the arrival of a great wave of eastern species of rodents from the European continent. Characteristic of this particular invasion of continental forms are *Spermophilus primigenius*, *Cricetus cricetus*, *Allocricetus bursae*, *Lagurus lagurus* and *Microtus nivalis*. In addition, there arrived three other boreal species, *Dicrostonyx torquatus*, *Lemmus lemmus* and *Microtus oeconomus*. During the coldest phase of this period all rodents connected with forest environment, including such adaptable species as *Clethrionomys glareolus* and *Apodemus sylvaticus*, apparently disappeared from the British Isles. The absence of *Microtus gregalis*, so common in Last Glaciation deposits, is a characteristic feature of the fauna of this stage.

The apparent occurrence of this cold stage between two interglacial stages with 'Ipswichian' floras is not in accordance with current palaeobotanical opinion, which identifies only one Ipswichian. The severity of this cold stage requires further assessment. The occurrence of both reindeer and wolverine, in addition to the above-mentioned rodent species, suggests more than a minor cool phase within an interglacial. Intense disturbance of the Glutton Stratum and the mixing of it with a vast quantity of fragments of broken stalagmite formations could be interpreted as evidence of very intense frost disturbance later than the Glutton Stratum but earlier than the deposition of the overlying layers. The relationship of this apparent cold stage to known glacial stages of the Upper Pleistocene (ice of the penultimate glaciation is believed to have reached north Devon) must remain, for the time being, unknown.

Other localities which Hinton (1926b) considered, from the rodent evidence, to be contemporaneous with Crayford are Clevedon and Banwell Caves. Cow Cave (part), Gough's Cave (part), Northfleet and Water Hall Farm (each with *Microtus nivalis*), and Hutton Cave (with cf. *Allocricetus bursae*) may be further examples of deposits approximately contemporaneous with the Glutton Stratum of Tornewton Cave.

Microtus nivalis apparently disappears from the British Pleistocene after this stage.

JOINT MITNOR INTERGLACIAL. The occurrence of a further interglacial stage with hippopotamus is reliably demonstrated at Tornewton Cave where the interglacial Hyaena Stratum overlies the Glutton Stratum. The occurrence of remains of *M. nivalis* and *M. oeconomus*, apparently underlying hippopotamus-bearing deposits, at Water Hall Farm gravel pit provides a further example of this relationship.

Important hippopotamus sites dating from this interglacial probably include Barrington, Joint Mitnor Cave and Swanton Morley. The rodent fauna of this stage is very sparse. The *Arvicola cantiana-terrestris* transition form and *Microtus agrestis* are the most common species. *Clethrionomys glareolus*, *Apodemus sylvaticus* and *Castor fiber* also occur. The Otter Stratum of Tornewton Cave (with the clawless otter, *Cyrnaonyx*, and white-toothed shrew, *Crocidura*, unknown elsewhere in the British Pleistocene) may represent the beginning of this stage, before the arrival of hippopotamus ; Minchin Hole appears to represent the end, after it had disappeared. The sparseness of this fauna suggests isolation of the British Isles from the European continent at that time.

Before leaving discussion of this interglacial, represented also by other sites such as Trafalgar Square with plant remains, we must refer once more to the Middle Terrace of the Thames interglacial, indistinguishable from it on palaeobotonical evidence. Evidence from the rodent remains nevertheless makes it difficult to explain the sequence other than with two post-Hoxnian interglacial stages separated by the Tornewton Glutton Stratum cold stage. The sequence becomes even more complicated if we consider the significance of the Baker's Hole cold stage. Was this the same as the Tornewton Cave Glutton Stratum cold stage or (if, as Carreck (*in litt.*) has suggested, it occurred between the Ilford and Crayford stages) does it represent yet another earlier cold stage within the 'Ipswichian', *sensu lato*?

There is at present no means of knowing to which of these warm stages the Ipswichian type locality of Bobbitshole belongs, although recent studies by Coope (1974) have showed very close similarities between the insects of this site and of Trafalgar Square, suggesting that it could be the later one. This is in agreement with the view of Evans (1971) who assigned the Ipswichian *sensu stricto* to his half-cycle 3W (see pp. 40–42).

LAST GLACIATION. The Last (Devensian) Glaciation opened the way for a new immigration. This time the immigrants included not only both species of lemmings but also two new arrivals, the ground squirrel *Spermophilus superciliosus* and the vole *Microtus gregalis*. *Cricetus*, *Lagurus* and *Allocricetus*, though present at this time in France, did not find their way back to Britain. *Arvicola* had by this time evolved to *A. terrestris* (Koenigswald's *Arvicola* fauna group 3, see pp. 100–101). *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis* are other species recorded and *M. arvalis* may have been present for a short time. *Castor fiber* apparently disappeared.

This fauna differs substantially from that of the preceding cold phase represented by the Glutton Stratum of Tornewton Cave, from which it is readily distinguishable. Diagnostic criteria include the absence of *Spermophilus primigenius* (found at Crayford), *Cricetus*, *Allocricetus*, *Microtus nivalis* and *Lagurus* and the appearance of *Spermophilus superciliosus* and *Microtus gregalis*. *Arvicola* had evolved from the *A. cantiana-terrestris* transition form to true *A. terrestris*. *Dicrostonyx*, *Lemmus* and *Microtus oeconomus* were present during both stages.

It is impossible at present to reconstruct in detail all the changes of the rodent fauna of the Last Glaciation. We have nevertheless now reached the most recent stage within the Quaternary, except for the Holocene, and the later part of it lies within the range of radiocarbon dating. Some changes of the rodent fauna are apparent, which offer a basis for more detailed study in the future, when more and better-dated material becomes available for study.

During the coldest part of the Last Glaciation *Apodemus sylvaticus* and perhaps also *Clethrionomys glareolus* disappeared from a large part or perhaps all of Britain. During the warmest interstadial the two lemmings were apparently absent, at least in the south of England.

Three sites with ^{14}C dates are of special importance. These are:

1. Willment's Pit, Isleworth, west London. 43 140 + 1520 or − 1280 years B.P. *Microtus oeconomus* and *M. gregalis* (possibly the earliest record of this species in Britain) occur; no lemmings.
2. Upton Warren, Worcestershire. 41 000 years B.P. *Dicrostonyx* present.
3. Beckford, Worcestershire. 27 650 ± 250 years B.P. Probably with *Microtus arvalis*.

Coope, who is making a detailed study of the insect faunas of the Last Glaciation, has named the period of time covered by the above sites the Upton Warren Interstadial complex. He found evidence (pers. comm.) of an intense and short amelioration of climate at about 43 000 years ago, followed by climatic deterioration with increase of continentality at about 41 000 years. The lack of lemmings at Isleworth is in accordance with the evidence provided by the insects. The Beckford insect fauna (pers. comm.) indicates cold conditions.

Other important Last Glaciation sites in the south of England, which lack lemmings, are Levaton Cave and Picken's Hole. The deposits of this last-mentioned site are interpreted by Stuart (1974) as possibly Early Devensian (layer 5, with *Microtus* cf. *oeconomus* and *M.* cf. *gregalis*) and Middle Devensian (layer 3, with *Citellus* sp. (= *Spermophilus* sp.) and *Microtus* cf. *gregalis*).

The best evidence of the rodent faunas of the end of the Last Glaciation and early Holocene is provided by the deposits of the Lea Valley and by the Peakland Archaeological Society's excavations in Dowel Cave, Etches' Cave and Fox Hole Cave. The end of the Pleistocene is marked by a special abundance of lemmings. Late Glacial deposits in the Lea Valley (dated on palaeobotanical evidence) contained both *Lemmus lemmus* and *Dicrostonyx torquatus* and also *Arvicola terrestris*, *M. oeconomus* and *M. anglicus* (= *M. gregalis*). Of these *Dicrostonyx torquatus* was still present in pollen Zone III (the last stage of the Pleistocene, ending about 10 000 years ago) and *M. oeconomus* survived into the Holocene. The cave sites mentioned above also indicate an abundance of lemmings in the Late Pleistocene. Other species present were *Arvicola terrestris*, *M. gregalis* and *M. oeconomus*, the last-mentioned species surviving there too into the Holocene.

At the end of the Last Glaciation arctic species of rodents began to disappear, though both *Lemmus* and *Dicrostonyx* seem to have survived at Nazeing until near the end of this period, the latter species still being present in pollen Zone III. *M. gregalis* does not appear to have persisted into post-Pleistocene times.

HOLOCENE. The postglacial rodent fauna is poorer than that of the neighbouring continent of Europe, but two species of rodents, now extinct in the British Isles, persisted. These are *Microtus oeconomus* and *Castor fiber*. *M. oeconomus* apparently continued in the Lea Valley until pollen Zone V, Mesolithic, about 9000 years ago. It also survived until Mesolithic times at Dowel Cave and was apparently present on the Isles of Scilly during the Bronze Age.

Castor fiber, apparently absent during the Last Glaciation, had already reappeared by about 9500 years ago (pollen Zone IV–V transition, Mesolithic, Star Carr), surviving until possibly the thirteenth century. Although the date of the Scottish finds is uncertain, *Castor fiber* may have reached Scotland during this stage.

Arvicola terrestris persisted from the Pleistocene and still occurs in Britain at the present day. In the Lea Valley *Apodemus sylvaticus, Clethrionomys glareolus* and *Microtus agrestis* reappeared in pollen Zone V–VI (about 9000 years ago) after an apparent interval at the end of the Pleistocene.

Sciurus vulgaris was probably a post-Pleistocene arrival. Others were *Apodemus flavicollis, Muscardinus avellanarius* and *Micromys minutus.* It is difficult to decide whether these last three species reached Britain with or without participation of human activity. Geological and ecological data suggest rather the second possibility. *Glis glis, Mus musculus, Rattus rattus* and *Rattus norvegicus* are evidently recent human introductions.

IRELAND. At some stage during the Last Glaciation the two species of lemmings, but no voles nor any steppe elements, managed to cross to Ireland. A ^{14}C date of 33 000 years for an associated mammoth bone from Castlepook Cave suggests that *Lemmus* and *Dicrostonyx* were probably established in Ireland at that time. Both are northern species which might be expected to reach Ireland in advance of other rodents. On the basis of existing evidence, the availability of lemmings for immigration from the British mainland appears entirely plausible.

Apodemus sylvaticus, recorded from the Pleistocene levels of Castlepook Cave, may also have arrived in Ireland during the Pleistocene, although it has been observed that at some cave sites this species was most abundant in the upper levels, suggesting a later date. Other rodent species which occur in Ireland today are probably post-Pleistocene arrivals.

V. ACKNOWLEDGEMENTS

The writers gratefully acknowledge help with the compilation of this Bulletin from many sources.

Dr W. von Koenigswald, of Tübingen University, advised on British representatives of the *Mimomys–Arvicola* lineage, and commented on the typescript.

Mr M. J. Bishop, of University College, London, provided us with full details of his determinations of the rodent remains from the Middle Pleistocene fissure deposit at Westbury-sub-Mendip and allowed us to see the typescript of his report on this site before publication.

Mr J. N. Carreck (Queen Mary College) read the typescript and provided many valuable suggestions. He also allowed us to mention important findings from his own unpublished studies in the Thames estuary.

Dr G. B. Corbet, of the British Museum (Natural History), provided determinations of rodent remains from Alveston Fissure, Beckford and Marlow and commented on the typescript.

Dr A. J. Stuart, of the University of Cambridge, provided determinations of rodent remains excavated in Minchin Hole in 1973 and much other help. He commented on our typescript and allowed us to see that of his review of British Pleistocene vertebrates before publication.

Dr J. d'A. Waechter provided an important collection of rodent remains excavated from the Lower Loam of Barnfield Pit, Swanscombe, during 1968–72.

Dr G. R. Coope, of Birmingham University, provided rodent remains from Beckford and advice on the events of the Last Glaciation in Britain.

Dr R. G. Wolff, of the University of Florida, provided details of rodent remains collected from Hoxne, Norfolk, by the University of Chicago under grants GS41435 and GS2907 of the National Science Foundation to Dr R. Singer.

Stratigraphic and other information was received from Mr D. Bramwell (Peakland Archaeological Society), Dr A. S. Clarke (Royal Scottish Museum, Edinburgh), Dr J. Jewell (British Museum (Natural History)), Mr D. Mayhew (Cambridge), Professor G. F. Mitchell (Trinity College, Dublin), Mr H. E. P. Spencer (Ipswich), Dr R. G. West and Mrs G. Wilson (University of Cambridge).

Mr J. J. Hooker sieved Pleistocene sediment from Aveley, Essex, for rodent remains, Mr J. Simons sediment from Willments Gravel Pit, Isleworth, London, and from Water Hall Farm Pit, Hertfordshire, all with important results.

Mr A. P. Currant (British Museum (Natural History)) prepared Figs 1, 5–18 and 21–31 and Mrs A. J. Sutcliffe drew Figs 2–4.

Mr D. L. F. Sealy provided much editorial help, including preparing the index, and Mrs M. N. M. Bhukhureea prepared the typescript with great patience.

VI. REFERENCES

An asterisk (*) distinguishes those papers cited in the text which are not directly concerned with Quaternary rodents of the British Isles.

ABBOT, W. J. L. 1917. The ossiferous fissures of the valley of the Shode. Appendix I *in*: BENNETT, F. J. *Ightham, The Story of a Kentish Village and its Surroundings*: 101–119, 1 pl., 2 tables, 1 fig. London.

* AGADZHANIAN, A. K. 1973. (Collared lemmings of the Pleistocene). *Nov. tekt. nov. otlozhi i chelovek*, Moscow, **5**: 320–355. [In Russian.]

APSIMON, A. M., DONOVAN, D. T. & TAYLOR, H. 1961. The stratigraphy and archaeology of the late-glacial and post-glacial deposits at Brean Down, Somerset. *Proc. speleol. Soc.*, Bristol, **9**: 67–136.

* AZZAROLI, A. 1953. The deer of the Weybourne Crag and Forest Bed of Norfolk. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **2**: 1–96.

BARRETT-HAMILTON, G. E. H. & HINTON, M. A. C. 1910–21. *A History of British Mammals* (unfinished). **1** (1910): xvi+263 pp., 20 pls. **2** (1911–21): 748 pp., 37 pls. London.

BATE, D. M. A. 1901. A short account of a bone cave in the Carboniferous Limestone of the Wye Valley. *Geol. Mag.*, London, (n.s. 4) **8**: 101–106.

BEIRNE, B. P. 1947. The history of the British Land Mammals. *Ann. Mag. nat. Hist.*, London, (11) **14**: 501–514.

BISAT, W. S. 1940. Older and Newer Drift in East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **24**: 137–151.

BISHOP, M. J. 1974. A preliminary report on the Middle Pleistocene mammal bearing deposit of Westbury-sub-Mendip, Somerset. *Proc. speleol. Soc.*, Bristol, **13**: 301–318.

—— 1975. Earliest record of Man's presence in Britain. *Nature, Lond.* **253**: 95–97.

BLACKMORE, H. P. & ALSTON, E. R. 1874. On Fossil Arvicolidae. *Proc. zool. Soc. Lond.* **1874**: 460–471, 3 figs.

BLORE, J. D. 1966. The excavation of Lynx Cave, 1962–1964. A preliminary report. *Newsl. Peakland archaeol. Soc.*, Stockport, **21** : 17–19, 35.

BOYLAN, P. J. 1967. The Pleistocene mammalia of the Sewerby–Hessle buried cliff, East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **36** : 115–125.

BRAMWELL, D. 1960. The vertebrate fauna of Dowel Cave – final report. *Newsl. Peakland archaeol. Soc.*, Stockport, **17** : [9–12, 23] (pages unnumbered).

—— 1964. The excavations at Elder Bush Cave, Wetton, Staffs. *North Staffs. J. Fld Studs*, Keele, **4** : 46–60.

—— 1970. The tenth report on Fox Hole Cave, High Wheeldon. *Bull. Peakland archaeol. Soc.*, Stockport, **25** : 8–10.

BREWSTER, T. C. M. 1963. *The Excavation of Staple Howe.* Malton, E. Riding Arch. Res. Cttee.

BROWN, J. 1852. On the Upper Tertiaries at Copford, Essex. *Q. Jl geol. Soc. Lond.* **8** : 184–193.

BURCHELL, J. P. T. 1935. Evidence of a further glacial episode within the valley of the Lower Thames. *Geol. Mag.*, London, **72** : 90–91.

* BURLEIGH, R. 1972. Carbon 14 dating with application to dating of remains from caves. *Stud. Speleol.*, London, **2** : 176–190.

CAMPBELL, J. B. & SAMPSON, C. G. 1971. A new analysis of Kent's Cavern, Devonshire, England. *Univ. Ore. anthrop. Pap.*, Eugene, Oregon, **3** : 1–40.

CARRECK, J. N. 1957. A late Pleistocene rodent and amphibian fauna from Levaton, near Newton Abbot, South Devon. *Proc. Geol. Ass.*, London, **68** : 304–308.

—— 1959. *In* : KERNEY, M. P. An interglacial tufa near Hitchin, Herts. *Proc. Geol. Ass.*, London, **70** : 322–337.

—— 1966. Microtine remains from the Norwich Crag (Lower Pleistocene) of Easton Bavents, Suffolk. *Proc. Geol. Ass.*, London, **77** : 491–496.

CATT, J. A. & PENNY, L. F. 1966. The Pleistocene deposits of Holderness, East Yorkshire. *Proc. Yorks. geol. Soc.*, Leeds, **35** : 375–420.

CHALINE, J. 1972. *Les Rongeurs du Pléistocène Moyen et Supérieur de France.* 410 pp., 17 pls. Paris.

CHEADLE, R. W. 1876. On mammalian bones recently found at Crayford and Erith. *Proc. W. Lond. scient. Ass. Fld Club* **1** : 70–71.

COLEMAN, J. C. 1965. *The Caves of Ireland.* 88 pp., 21 figs, 8 pls. Tralee.

* COOPE, G. R. 1974. Interglacial Coleoptera from Bobbitshole, Ipswich, Suffolk. *J. geol. Soc. Lond.* **130** : 333–340.

* —— 1975. An ecological study of a temperate interlude in the middle of the Last Glaciation, based on Coleoptera from Isleworth, Middlesex. *J. anim. Ecol.*, London. **44** : 365–391.

——, SHOTTON, F. W. & STRACHAN, I. 1961. A late Pleistocene fauna and flora from Upton Warren, Worcestershire. *Phil. Trans. R. Soc.*, London, B **244** : 379–421.

* CORBET, G. B. 1961. Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. *Nature, Lond.* **191** : 1037–1040.

* —— 1966. *The Terrestrial Mammals of Western Europe.* xi+264 pp. London.

* ——, CUMMINS, J., HEDGES, S. R. & KRZANOWSKI, W. 1970. The taxonomic status of British water voles, genus *Arvicola*. *J. Zool., Lond.* **161** : 301–316.

CRANBROOK, LORD 1955a. Fossil Voles. *Trans. Suffolk Nat. Soc.*, Ipswich, **9** : 48–49, 3 figs [published anonymously].

—— 1955b. Records of *Mimomys*. *Trans. Suffolk Nat. Soc.*, Ipswich, **9** : 58 [published anonymously].

DAVIES, J. A. 1921. Aveline's Hole, Burrington Combe. *Proc. speleol. Soc.*, Bristol, **1** : 61–68.

DAWKINS, W. B. & SANFORD, W. A. 1866–72. British Pleistocene Mammalia, **1** (Felidae). l+194 pp., 26 pls. *Palaeontogr. Soc.* (*Monogr.*), London.

* DIENSKE, H. 1969. Notes on difference between some external and skull characters of *Microtus arvalis* (Pallas, 1778) and of *Microtus agrestis* (Linnaeus, 1761) from the Netherlands. *Zöol. Meded. Leiden* **44** (6) : 83–108.

* Ellerman, J. R. & Morrison-Scott, T. C. S. 1966. *Checklist of Palaearctic and Indian Mammals*. 2nd ed. 810 pp., map. London, British Museum (Natural History).

* Evans, P. 1971. Towards a Pleistocene time-scale. *In*: The Phanerozoic Time-scale – a Supplement. *Spec. Publs geol. Soc. Lond.* **5**: 123–351.

Evans, W. 1907. Mammals of the Edinburgh or Forth area. *Proc. R. phys. Soc. Edinb.* **16**: 387–405.

—— 1913. Lemming remains in south-east Scotland. *Scott. Nat.*, Edinburgh, **17**: 97–100, 1 fig.

* Fahlbusch, V. 1969. Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. *Acta zool. cracov.* **14** (5): 99–137, pls 8–18.

Falconer, H. See Murchison, C. 1868.

* Franks, J. W. 1960. Interglacial deposits at Trafalgar Square, London. *New Phytol.*, Oxford, **59**: 145–152.

Fraser, F. C. & King, J. E. 1954. Faunal remains. Ch. 3 *in*: Clark, J. G. D. *Excavations at Star Carr*: 70–95. Cambridge.

Friant, M. 1962. Sur le *Castor plicidens* F. Maj. de l'époque des Palafittes. *Jb. naturh. Mus. Bern* **1960–62**: 117–125, pls 1–2.

* Giebel, C. G. A. 1847. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere* **1** (1), Die Säugethiere. 467 pp. Leipzig.

* Gromov, I. M. 1965. *In*: Gromov, I. M., Bibikov, D. I., Kalabukhov, N. I. & Meier, M. N. Nezemnye belichi (Marmotinae). *Fauna SSSR*, Moscow & Leningrad, **3** (2): 1–466.

Hinton, M. A. C. 1900a. On the Pleistocene deposits of the Ilford and Wanstead district, Essex. *Essex Nat.*, Buckhurst Hill, **11**: 161–165.

—— 1900b. The Pleistocene deposits of the Ilford and Wanstead district. *Proc. Geol. Ass.*, London, **16**: 271–281.

—— 1901. Excursion to Grays Thurrock. *Proc. Geol. Ass.*, London, **17**: 141–144.

—— 1907a. On the existence of the alpine vole (*Microtus nivalis* Martins) in Britain during Pleistocene times. *Proc. Geol. Ass.*, London, **20**: 39–58.

—— 1907b. Note on the occurrence of the alpine vole (*Microtus nivalis*) in the Clevedon Cave deposit. *Proc. Bristol Nat. Soc.* (4) **1**: 190–191.

—— 1910a. Some new late Pleistocene voles and lemmings. *Ann. Mag. nat. Hist.*, London, (8) **6**: 34–39.

—— 1910b. A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. *Proc. Geol. Ass.*, London, **21**: 489–507.

—— 1912. Note on the lemming remains from the Arctic Bed at Angel Road. *In*: Warren, S. H. A Late Glacial stage in the valley of the River Lea. *Q. Jl geol. Soc. Lond.* **68**: 249.

—— 1914. On some remains of rodents from the Red Crag of Suffolk. *Ann. Mag. nat. Hist.*, London, (8) **13**: 186–195, 1 pl.

—— 1915. Note on British fossil species of Apodemus. *Ann. Mag. nat. Hist.*, London, (8) **15**: 580–584.

—— 1920. Description of the rodent teeth. *In*: Trechmann, C. T. On a deposit of interglacial loess and some transported pre-glacial clays on the Durham Coast. *Q. Jl geol. Soc. Lond.* **75**: 201.

—— 1921. Note on the remains of small mammals obtained from Aveline's Hole, Burrington Combe, Somerset. *Proc. speleol. Soc.*, Bristol, **1**: 74–78.

—— 1923a. Diagnoses of species of *Pitymys* and *Microtus* occurring in the Upper Freshwater Bed of West Runton, Norfolk. *Ann. Mag. nat. Hist.*, London, (9) **12**: 541–542.

—— 1923b. Note on the rodent remains from Clacton-on-Sea. *Q. Jl geol. Soc. Lond.* **79**: 626.

—— 1924. Notes on the rodent remains from Aveline's Hole. *Proc. speleol. Soc.*, Bristol, **2**: 34–37.

—— 1925. Preliminary note upon the mammalian remains from Merlin's Cave. *Proc. speleol. Soc.*, Bristol, **2**: 156–158.

—— 1926a. The Pleistocene mammalia of the British Isles and their bearing upon the date of the glacial period. *Proc. Yorks. geol. Soc.*, Leeds, (n.s.) **20**: 325–348.

Hinton, M. A. C. 1926b. *Monograph of the Voles & Lemmings (Microtinae) Living and Extinct.* **1** : xvi+488 pp., 15 pls, 110 figs. London, British Museum (Natural History).

—— 1952. *In* : Allison, J., Godwin, H. & Warren, S.H. Late-glacial deposits at Nazeing in the Lea Valley, North London. *Phil. Trans. R. Soc.*, London, B **236** : 169–240.

——, Kennard, A. S. & Newton, E. T. 1900. Contributions to the Pleistocene geology of the Thames Valley. I. The Grays Thurrock area, part 1. *Essex Nat.*, Buckhurst Hill, **11** : 336–370.

—— & White, G. 1902. Note on the occurrence of *Microtus intermedius* in the Pleistocene deposits of the Thames Valley. *Proc. Geol. Ass.*, London, **17** : 414–415.

Jackson, J. W. 1909. On the discovery of the remains of lemmings in Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **2** : 227–229.

—— 1910. On the vertebrate fauna found in the cave-earth at Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **2** : 323–332.

—— 1912. Additional notes on the Pleistocene fauna of Dog Holes, Warton Crag. *Lancs. Nat.*, Darwen, **4** : 420–422.

—— 1929a. Remains of lemmings in Derbyshire caves. *Naturalist, Hull* **1929** : 105–107.

—— 1929b. Report on the animal remains found in Kilgreany Cave, Co. Waterford. *Proc. speleol. Soc.*, Bristol, **3** : 137–152.

—— 1932. [*Dicrostonyx* in Welsh caves.] *Proc. Dyserth Distr. Fld Club*, Llanfairfechan, **54** [not seen].

—— 1934. The rodent remains from the Pin Hole Cave. *Rep. Br. Ass. Advmt Sci.*, Aberdeen : 256–257.

—— 1947. The Upper Pleistocene fauna and its relation to the Ice Age. *Proc. Lpool geol. Soc.* **19** : 165–183.

* Janossy, D. 1954. Fossile Microtinen aus dem Karpathenbecken. I. Lemminge. *Annls hist.-nat. Mus. natn. hung.*, Budapest, n.s. **5** : 39–48, 1 pl.

* —— 1961. Die Entwicklung der Kleinsäugerfauna im Pleistocän (Insectivora, Rodentia, Lagomorpha). *Z. Säugetierk.*, Berlin, **26** : 1–11.

* —— 1962. Vorläufige Mitteilung über die Mittelpleistozäne Vertebratenfauna der Tarkö-Felsnische (NO-Ungarn, Bükk-Gebirge). *Annls hist.-nat. Mus. natn. hung.*, Budapest, **54** : 155–176.

Johnson, J. P. & White, G. 1900. Some new sections in, and contributions to, the fauna of the river drift of the Uphall estate, Ilford, Essex. *Essex Nat.*, Buckhurst Hill, **11** : 157–160.

* Kaup, J. J. 1839. *Description d'Ossements Fossiles de Mammifères* (&c.) **5** : 91–119. Darmstadt.

Kennard, A. S. 1944. The Crayford brickearths. *Proc. Geol. Ass.*, London, **55** : 121–169.

—— 1945–46. The early digs in Kent's Hole, Torquay, and Mrs Cazalet. *Proc. Geol. Ass.*, London, **56** : 156–213.

Kerney, M. P. 1971. Interglacial deposits in Barnfield Pit, Swanscombe, and their molluscan fauna. *J. geol. Soc.*, London, **127** : 69–93.

* King, W. B. R. & Oakley, K. P. 1936. The Pleistocene succession in the lower parts of the Thames Valley. *Proc. prehist. Soc.*, Cambridge, (n.s.) **2** : 52–76.

* Koenigswald, W. von 1970. Mittelpleistozäne Kleinsäugerfauna aus der Spaltenfüllung Petersbuch bei Eichstätt. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **10** : 407–432.

—— 1972. Sudmer-Berg-2, eine Fauna des frühen Mittelpleistozäns aus dem Harz. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **141** : 194–221.

—— 1973. Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistocän). *Eiszeitalter Gegenw.*, Ohringen, **23–24** : 159–167.

* Kormos, T. 1934. Neue Insectenfresser, Fledermäuse und Nager aus dem Oberpliocän der Villányer Gegend. *Földt. Közl.*, Budapest, **64** : 296–321.

Kowalski, K. 1966. Stratigraphic importance of rodents in the studies on European Quaternary. *Folia quatern.*, Krakow, **22** : 1–16.

—— 1967. *Lagurus lagurus* (Pallas 1773) and *Cricetus cricetus* (Linnaeus 1758) (Rodentia, Mammalia) in the Pleistocene of England. *Acta zool. cracov.* **12** : 111–122, 24 figs.

* —— 1970. Variation and speciation in fossil voles. *Symp. zool. Soc. Lond.* **26** : 149–160.

Kretzoi, M. 1958. New names for Arvicolid homonyms. *Annls hist.-nat. Mus. natn. hung.*, Budapest, **50** : 55–58.

—— 1965. Die Nager und Lagomorphen von Voigstedt in Thüringen und ihre chronologische Aussage. *Paläont. Abh. Berl.* A **11** : 585–660, 2 pls, 2 figs.

* Kurtén, B. 1969. *Pleistocene Mammals of Europe.* viii + 317 pp. London.

Lamplugh, G. W. 1891. Final report of the Committee . . . appointed for the purpose of investigating an ancient sea-beach near Bridlington Quay. *Rep. Br. Ass. Advmt Sci.*, Leeds : 375–377.

Lankester, E. R. 1864. On new mammalia from the Red Crag. *Ann. Mag. nat. Hist.*, London, **14** : 353–360, pl. 8.

* Laugel, A. 1862. La faune de Saint-Prest près Chartres (Eure et Loire). *Bull. Soc. géol. Fr.*, Paris, (2) **19** : 709–718, 3 figs.

* Lehmann, U. 1953. Eine Villafranchiano-Fauna von der Erpfingen Höhle (Schwäb. Alb). *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, B **1953** : 437–464.

* —— 1957. Weitere Fossilfunde aus dem ältesten Pleistocän der Erpfingen Höhle (Schwäbische Alb.). *Mitt. geol. StInst. Hamb.* **26** : 60–99.

Lydekker, R. 1885–87. *Catalogue of the Fossil Mammalia in the British Museum (Natural History).* **1** (Primates, Chiroptera, Insectivora, Carnivora and Rodentia), 1885, xxx + 268 pp. **5** (Tillodontia, Sirenia, Cetacea, Edentata, Marsupialia, Monotremata and Supplement), 1887, xxxv + 345 pp. London.

Lyell, C. 1840. On the Boulder Formation or drift and associated freshwater deposits composing the mud cliffs of eastern Norfolk. *Lond. Edinb. phil. Mag.*, London, (3) **16** : 345–380, 18 figs.

Major, C. I. F. 1902. [Exhibition of, and remarks upon, some jaws and teeth of Pliocene voles (*Mimomys*, gen. nov.).] *Proc. zool. Soc. Lond.* **1902** (1) : 102–107.

—— 1908a. The mammalian fauna of the Forest Bed. *Geol. Mag.*, London, (5) **5** : 329–330.

—— 1908b. On species of *Castor*, fossil and recent. *Proc. zool. Soc. Lond.* **1908** : 630–635.

* Mandach, E. V. 1938. Skelettreste von *Dicrostonyx groenlandicus* Trail als Inhalt von Raubvogelgewöllen. *Meddr Grønland*, Copenhagen, **112** (4) : 1–54, 22 pls.

* Matthews, L. H. 1952. *British Mammals.* xii + 410 pp., 16 + 48 pls. London.

* Méhely, L. v. 1914. Fibrinae Hungariae. Die ternären und quartären Wurzelzähnigen Wühlmause Ungarns. *Annls hist.-nat. Mus. natn. hung.*, Budapest, **12** : 155–243.

* Miller, G. S. 1912. *Catalogue of the Mammals of Western Europe.* xv + 1019 pp. London, British Museum.

Mitchell, G. F. 1969. Pleistocene mammals in Ireland. *Bull. Mammal Soc. Br. Isl.*, Birmingham, **31** : 21–25.

* ——, Penny, L. F., Shotton, F. W. & West, R. G. 1973. A correlation of Quaternary deposits in the British Isles. *Spec. Rep. geol. Soc. Lond.* **4** : 99 pp.

Montagu, I. 1924. On the remains of Fen Beaver in the Sedgwick Museum. *Proc. zool. Soc. Lond.* **1924** : 1081–1086.

Mullins, E. H. 1913. The ossiferous cave at Langwith. *J. Derbysh. archaeol. nat. Hist. Soc.*, Derby, **35** : 137–153, 6 pls.

Murchison, C. (ed.) 1868. *Palaeontological memoirs and notes of the late Hugh Falconer.* **1** : lvi + 590 pp., 34 pls. **2** : xiii + 675 pp., 38 pls. London.

Nehring, A. 1875. Fossile Lemminge und Arvicolen aus den Diluviallehm von Thiede bei Wolfenbüttel. *Z. ges. Naturw.*, Berlin, **45** : 1–28, pl. I.

Newton, E. T. 1881. Notes on the Vertebrata of the pre-glacial Forest Bed Series of the East of England. *Geol. Mag.*, London, (2) **8** : 256–259.

—— 1882a. The Vertebrata of the Forest Bed Series of Norfolk and Suffolk. viii + 143 pp., 19 pls. *Mem. geol. Surv. U.K.*, London.

—— 1882b. On the occurrence of *Spermophilus* beneath the glacial till of Norfolk. *Geol. Mag.*, London, (n.s. 2) **9** : 51–54, pl. 2.

—— 1890a. On the occurrence of lemmings and other rodents in the brick-earth of the Thames Valley. *Geol. Mag.*, London, (n.s. 3) **7** : 452–455, 8 figs.

Newton, E. T. 1890b. On some new mammals from the Red and Norwich Crags. *Q. Jl geol. Soc. Lond.* **46** : 444–453, pl. 18.

—— 1891. The Vertebrata of the Pliocene deposits of Britain. xi + 137 pp., 10 pls. *Mem. geol. Surv. U.K.*, London.

—— 1892. On a skull of *Trogontherium cuvieri* from the Forest Bed of East Runton, near Cromer. *Trans. zool. Soc. Lond.* **13** : 165–175, pl. 19.

—— 1894. The vertebrate fauna collected by Mr Lewis Abbot from the fissure near Ightham, Kent. *Q. Jl geol. Soc. Lond.* **50** : 188–210, pls 10–12.

—— 1899a. [Exhibition of remains of *Mus Lewisi* from Ightham.] *Proc. zool. Soc. Lond.* **1899** : 381.

—— 1899b. Additional notes on the vertebrate fauna of the rock-fissure at Ightham (Kent). *Q. Jl geol. Soc. Lond.* **55** : 419–429, pl. 28.

—— 1902. *Trogontherium* from a Pleistocene deposit in the Thames Valley. *Geol. Mag.*, London, (n.s. 4) **9** : 385–388.

—— 1909. Hamster remains from the Norfolk Forest Bed. *Geol. Mag.*, London, (5) **6** : 110–113.

—— 1916. *Trogontherium* from the Pleistocene of Copford, Essex. *Geol. Mag.*, London, (6) **3** : 322–323, 4 figs.

* Norton, P. E. P. 1967. Marine Mollusca in the Early Pleistocene of Sidestrand and the Royal Society borehole at Ludham, Norfolk. *Phil. Trans. R. Soc.*, London, B **253** : 161–200.

* Oken, L. 1815–16. *Okens Lehrbuch der Naturgeschichte. III Zoology* **1** : xxviii + 842 + xviii + iv pp., 40 pls. **2** : xvi + 1270 + (2) pp., 1 tab. ; pp. 843–50 (suppl. to **1**).

Osborn, H. F. 1922. Pliocene (Tertiary) and early Pleistocene (Quaternary) mammalia of East Anglia, Great Britain, in relation to the appearance of Man. *Geol. Mag.*, London, **59** : 433–441.

* Ovey, C. D. (ed.) 1964. The Swanscombe Skull. *Occ. Pap. R. anthrop. Inst.*, London, **20** : xii + 215 pp., 25 pls.

Owen, R. 1846. *A History of British Fossil Mammals, and Birds.* xlvi + 560 pp., 236 figs. London.

—— 1869. On the distinction between *Castor* and *Trogontherium*. *Geol. Mag.*, London, **6** : 49–56, pl. 3, 4 figs.

Palmer, L. S. 1934. Some Pleistocene breccias near the Severn Estuary. *Proc. Geol. Ass.*, London, **45** : 145–161.

Pasquier, L. 1972. Étude d'une population de *Mimomys savini* Hinton, 1910 (Arvicolidae, Rodentia) provenant de l'Upper Freshwater Bed (Quaternaire Ancien d'Angleterre). *Mammalia*, Paris, **36** : 214–225.

Peach, B. N. & Horne, J. 1917. The bone cave in the valley of Allt nan Uamh (Burn of the Caves) near Inchnadamph, Assynt, Scotland. *Proc. Roy. Soc. Edinb.* **37** : 327–349.

Pernetta, J. C. 1966. Report on the findings at Etches' Cave, Dowel Dale, Derbyshire. *Newsl. Peakland archaeol. Soc.*, Stockport, **21** : 11–16, 35.

—— & Handford, P. T. 1970. Mammalian and avian remains from possible Bronze Age deposits on Nornour, Isles of Scilly. *J. Zool., Lond.* **162** : 534–540.

* Pike, K. & Godwin, H. 1952. The interglacial at Clacton-on-Sea. *Q. Jl geol. Soc. Lond.* **108** : 261–272.

* Pomel, A. 1848. Description de la tête du Castoroides Ohioensis Forster par Wyman. *Archs Sci. phys. nat.*, Geneva, **9** : 165–167.

* Reichstein, H. 1963. Beitrag zur systematischen Gliederung des Genus *Arvicola* Lacépède 1799. *Z. Zool. Syst. EvolForsch.*, Frankfurt a.M., **1** : 155–204.

Reid, C. 1890. The Pliocene deposits of Britain. viii + 326 pp., 5 pls, 48 figs. *Mem. geol. Surv. U.K.*, London.

* Rzebik, B. 1968. *Crocidura* Wagler and other Insectivora (Mammalia) from the Quaternary deposits of Tornewton Cave in England. *Acta zool. cracov.* **13** : 251–263.

Sanford, W. A. 1870a. On the rodentia of the Somerset caves. *Proc. Somerset archaeol. nat. Hist. Soc.*, Taunton, **1868–69** : 51–57, 1 pl.

SANFORD, W. A. 1870b. On the rodentia of the Somerset caves. *Q. Jl geol. Soc. Lond.* **26** : 124–131.

SAVAGE, R. J. G. 1963. Martin Alister Campbell Hinton, 1883–1961. *Biogr. Mem. Fellows R. Soc.*, London, **9** : 155–170, 1 pl.

—— 1966. Irish Pleistocene mammals. *Ir. Nat. J.*, Belfast, **15** : 117–130.

SCHARFF, R. F. 1906. The exploration of the caves of County Clare. *Trans. R. Ir. Acad.*, Dublin, B **33** : 1–76.

——, COFFEY, G., COLE, G. A. J. & USSHER, R. J. 1903. The exploration of the Caves of Kesh, County Sligo. *Trans. R. Ir. Acad.*, Dublin, B **32** : 171–214, pls 9–11.

——, SEYMOUR, H. J. & NEWTON, E. T. 1918. The exploration of Castlepook Cave, County Cork. *Proc. R. Ir. Acad.*, Dublin, B **34** : 33–72 + map.

* SCHAUB, S. 1930. Quartäre und jungtertiäre Hamster. *Abh. schweiz paläont. Ges.*, Basel, **49** (6) : 1–49, 2 pls.

SCHLOSSER, M. 1902. Beiträge zur Kenntniss der Säugetierreste aus den süddeutschen Bohnerzen. *Geol. palaeont. Abh.*, Berlin, **9** : 117–258, 5 pls.

SCHREUDER, A. 1929. *Conodontes* (*Trogontherium*) and *Castor* from the Tegelen Clay, compared with Castoridae from other localities. *Archs Mus. Teyler*, Haarlem, (3) **6** : 99–320, 16 pls, 16 figs.

—— 1931. *Conodontes, Trogontherium* and other Castoridae. *Palaeont. Z.*, Berlin, **13** : 148–176, 6 figs.

—— 1950. Microtinae from the Middle Gravels of Swanscombe. *Ann. Mag. nat. Hist.*, London, (12) **3** : 629–635.

—— 1951. The three species of *Trogontherium* with a remark on *Anchitheriomys*. *Archs néerl. Zool.*, Leiden, **8** : 400–433, pls 20–23.

* SIDOROWICZ, J. 1964. Comparison of the morphology of representatives of the genus *Lemmus* Link, 1795, from Alaska and the Palaearctic. *Acta theriol.*, Białowieża, **8** : 217–226.

SINGER, R., WYMER, J., GLADFELTER, B. G. & WOLFF, R. G. 1973. Excavation of the Clactonian industry at the golf course, Clacton-on-Sea, Essex. *Proc. prehist. Soc.*, Cambridge, **39** : 6–74.

* SOUTHERN, H. N. (ed.) 1964. *The Handbook of British Mammals.* xxi + 465 pp., 60 pls. Oxford.

* SPARKS, B. W. & WEST, R. G. 1972. *The Ice Age in Britain.* xvii + 302 pp., 44 pls, figs. London.

SPENCER, H. E. P. 1956. The Hoxne mammalian remains. *In* : WEST, R. G. The Quaternary deposits at Hoxne, Suffolk. *Phil. Trans. R. Soc.*, London, B **239** : 265–365.

—— 1964. The contemporary mammalian fossils of the Crags. *Trans. Suffolk Nat. Soc.*, Ipswich, **12** : 333–344.

—— 1966. New mammalian fossils from the Red Crag. *Trans. Suffolk Nat. Soc.*, Ipswich, **13** : 154–156.

STEVENS, E. T. 1869. Drift series – mammalian remains. *In* : *Some Account of the Blackmore Museum* **2** : 109–115. Devizes.

STOPES, C. 1904. Palaeolithic implements from the Shelly Gravel Pit at Swanscombe, Kent. *Rep. Br. Ass. Advmt Sci.*, Southport : 803–804.

STRINGER, C. B. 1975. A preliminary report on new excavations at Bacon Hole Cave. *Gower*, Swansea, **26** : 32–37.

STUART, A. J. 1974. Pleistocene history of the British vertebrate fauna. *Biol. Rev.*, Cambridge, **49** : 225–266.

* SUTCLIFFE, A. J. 1960. Joint Mitnor Cave, Buckfastleigh. *Trans. Torquay nat. Hist. Soc.* **13** (1) : 1–26.

—— 1964. The mammalian fauna. *In* : OVEY, C. D. (ed.), The Swanscombe Skull. *Occ. Pap. R. anthrop. Inst.*, London, **20** : 85–111.

—— & BOWEN, D. Q. 1973. Preliminary report on excavations in Minchin Hole, April–May 1973. *Newsl. Pengelly Cave Stud. Trust* **21** : 12–25.

SUTCLIFFE, A. J. & COLLINGS, H. D. 1972. Gnawed bones from the Crag and Forest Bed of East Anglia. *Suffolk nat. Hist.*, Ipswich, **15** : 497–498.

—— & ZEUNER, F. E. 1962. Excavations in the Torbryan Caves, Devonshire. I. Tornewton Cave. *Proc. Devon archaeol. Explor. Soc.*, Torquay, **5** : 127–145, pls 26–27.

* TURNER, C. 1970. The Middle Pleistocene deposits at Marks Tey, Essex. *Phil. Trans. R. Soc.*, London, B **257** : 373–440.

USSHER, R. J. 1910. Cave hunting. *Ir. Nat.*, Dublin, **19** : 37–43.

——, SEYMOUR, H. J., NEWTON, E. T. & SCHARFF, R. F. 1908. On the Cave of Castlepook, near Doneraile, Co. Cork. *Rep. Br. Ass. Advmt Sci.*, Dublin : 697 ; *Geol. Mag.*, London (5) **5** : 462–463 ; *Ir. Nat.*, Dublin, **17** : 231–232.

* VIRET, J. 1954. Le loess à bancs durcis de Saint-Vallier. *Nouv. Archs Mus. Hist. nat. Lyon* **4** : 1–200, 33 pls.

WARREN, S. H. 1916. Further observations on the Late Glacial, or Ponders End, stage of the Lea Valley. *Q. Jl geol. Soc. Lond.* **71** : 164–182.

—— 1955. The Clacton (Essex) Channel deposits. *Q. Jl geol. Soc. Lond.* **111** : 283–307.

* WEST, R. G. 1961. The Glacial and Interglacial deposits of Norfolk. *Trans. Norfolk Norwich Nat. Soc.* **19** : 365–375.

—— 1968. *Pleistocene Geology and Biology* (&c.). xiii + 377 pp., 16 pls, figs. London.

* —— 1969. Pollen analyses from interglacial deposits at Aveley and Grays, Essex. *Proc. Geol. Ass.*, London, **80** : 271–282.

* —— 1972. Land–sea-level changes during the Pleistocene. *In* : A discussion on problems associated with the subsidence of southeastern England. *Phil. Trans. R. Soc.*, London, A **272** : 87–98.

* ——, LAMBERT, A. & SPARKS, R. W. 1964. Interglacial deposits at Ilford, Essex. *Phil. Trans. R. Soc.*, London, B **247** : 185–212.

* —— & WILSON, D. G. 1966. Cromer Forest Bed Series. *Nature, Lond.* **209** : 497–498.

WHITAKER, W. 1889. The geology of London and of part of the Thames Valley **1**. ix + 556 pp. *Mem. geol. Surv. U.K.*, London.

* WYMER, J. 1957. A Clactonian flint industry at Little Thurrock, Grays, Essex. *Proc. Geol. Ass.*, London, **68** : 159–177.

—— 1962. Excavations at the Maglemosian sites at Thatcham, Berkshire, England. *Proc. prehist. Soc.*, Cambridge, **28** : 329–361.

* —— 1974. Clactonian and Acheulean industries in Britain – their chronology and significance. *Proc. Geol. Ass.*, London, **85** : 391–421.

ZEUNER, F. E. 1945–59. *The Pleistocene Period, its Climate, Chronology and Faunal Successions.* 1st edition (1945), 322 pp. London (Ray Society). 2nd edition (1959), 447 pp., 80 figs. London.

* —— 1954. Riss or Würm? *Eiszeitalter Gegenw.*, Ohringen, **4–5** : 98–105.

ZIMMERMANN, K. 1959. Über eine Kreuzung von Unterarten der Feldmaus *Microtus arvalis*. *Zool. Jb.*, Jena, (Abt. Syst.) **87** : 1–12.

VII. INDEX

The page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure. Tab. 12 faces p. 122.

Acheulean industry 50–1
Africa 82
alder 52
Alice and Gwendoline Caves 68 ; see Edenvale
Allocricetus 66, 86–7, 127
  cf. *bursae* 63–4, 66, **86–7**, 101, tab. 12, 125–6
Allophaiomys pliocaenicus 105–7, 122
alluvial deposits 41, 53, 74, tab. 12 ; see localities
Alopex see fox (arctic)
Alston, E. R. 37
Alveston Fissure 45, 67, 93, 110, tab. 12, 129
amphibia 59
Angel Road 45, 59, 88, tab. 12
Anglian 41–2, 47–8, 76, 106, 123
Antian 41, 43

Apodemus 81–4
  flavicollis 62, 67, 70–1, **83–4**, tab. 12, 129
  lewisi 83–4
  sylvaticus 48, 52–3, 59, 61, 63–72, **81–3**, tab. 12, 122–7, 129
  whitei **52**, 81–3
  sp. 69, 81, 83
Arctic Freshwater Bed 48
Arvicola 37–9, 52–3, 64, 69, **99–102**, 103–5; see *Mimomys–Arvicola* lineage
  faunas 61, 100–1, tab. 12, 124, 127
  abbotti 103
  agrestis 109
  amphibia 37, 102–3
  amphibius 95, 98, 102–3
    terrestris 103
  arvalis 37, 106
  arvaloides 106
  bactonensis 48, 100, 102, 104
  cantiana 48, 51–3, 57, 60–2, 69, 72, 100*, 101, **102–3**, 104–5, tab. 12, 122–5
  cantiana-terrestris transition form 60, 64–5, 67, 69, 72, 100*, 101–2, **103**, 125–7
  cantiana/terrestris complex **104–5**
  glareolus 92
  greeni 48, 62, 100, 102, 104–5
  gregalis 107, 118
  gulielmi 37, 87
  intermedia 37, 95, 98–9
  praeceptor 53, 100, 102, 104
  pratensis 92
  ratticeps 117
  riparia 92
  sapidus 99
  terrestris 37, 59, 62, 64–5, 69–71, 99, 100*, 101–2, **103–4**, 105, tab. 12, 127–9
  sp. 54, 63–7, 69, 72, 125
Asia 76, 80, 82, 84–5, 87, 89, 94, 100, 105, 112, 118, 120–1
Asia Minor 78
Astian 41, 43, 78, 81
Austria 106, 109, 118
Aveley 45, 49–50, 53, 55–7, 69, 93, 101–2, tab. 12, 125–6, 130
Aveline's Hole 45, 70–1, 81, 83–4, 88, 90, 93, 104, 110, 112, 117–8, tab. 12
Avon, Warwickshire 72
Azov Sea 79

Bacon Hole 45, 67, 81, 93, 104, 110, 117
Bacton 45, 46*, 48, 78–9, 104, tab. 12
Baker's Hole 49–50, **59–60**
  cold stage 127
Ballymote 45
Ballynamintra Cave 45, 68, 82, 88, tab. 12
bank vole see *Clethrionomys*
Banwell Cave 45, 66, tab. 12, 126
Barnfield Pit 51–3, 80, 90, 92–3, 101–2, tab. 12, 123–4, 130; see Swanscombe
Barntick Cave 68, 82; see Edenvale
Barrington 45, 69, 72, 101–3, 110, tab. 12, 126
Bath 112
Baventian 41, 43
Beaker Age 71
bear 60, 62–3, 65
  brown 63–4, 68
Bear Stratum (Tornewton Cave) 63–4, 66
beaver 37, 39, 81; see *Castor*, *Trogontherium*
Beccles 45
Beckford 45, 72, 113, tab. 12, 128–30
Beestonian 41, 47–8, tab. 12
Belgium 83, 96
Bering Strait 92, 120
Berkshire 45; see Thatcham
Berwickshire 45; see Middlestots Bog
Betfia, Romania 95
Bhukhureea, Mrs M. N. M. 130
Biedermann'scher Stbr. 101
birch 56
birds of prey 60, 69; see owls
Bishop, M. J. 108, 129
bison 56
Black Mould (Kent's Cavern) 62
Blackmore, H. P. 37
Bleadon Cave 45, 70–1, 76–7, 110, 117, 119, tab. 12
Bobbitshole 45, 69, 72, 104, 110, tab. 12, 127
Bos see ox, giant
bovids 62–3
Bramerton 43, 45, 46*, 95, 98, tab. 12
Bramwell, D. 130
Brandon 89
Brassington 45
Brean Down 45, 72, 88, 110, tab. 12
Breccia (Kent's Cavern) 62, tab. 12
brickearth 48, 50, 53–4, 56–8
Briggs, D. J. 72, 113
Bristol Museum 107
Bristol University Spelaeological Society 81, 88, 91
British Museum (Natural History) 36, 58, 60–1, 66, 72, 97–8, 102, 107, 113, 116, 119
Brixham Cave 45, 70–1, 93, 104, 110, 112–3, 119, tab. 12
Bronze Age 128; see Nornour

Buckfastleigh 45
Buckinghamshire 45 ; see Marlow
Burchell, J. P. T. 60
Burrington 45
Burwell 45
Buxton 45

Calcareous Group (Westbury) 60–1, 122, 124
Cambridge Fens 45, 72, 80, tab. 12
Cambridge, P. 96 (footnote)
Cambridgeshire 45 ; see localities
Canada 92 ; see North America
Canis see wolf
  lupus mosbachensis 61
Cappagh 45
carbon-14 (^{14}C) dated sites 36, 58, 68–9, 72, 113, tab. 12, 127–9
Carnforth 45
Carrant Brook 72
Carreck, J. N. 50, 54, 56, 59–60, 69, 89, 91, 93, 104, 110, 127, 129
Castlepook Cave 45, 68–9, 82, 88, 91, tab. 12, 129
Castletownroche Cave 45, 68–9, 88, 91, tab. 12
Castor 39, 54, 69, 79–81
  europaeus 79
  fiber 37, 43, 47–8, 52–3, 61–2, 70–3, **79–81**, tab. 12, 122–8
    plicidens 81
  plicidens 79–81
  trogontherium 78
  veterior 79–80
  sp. 53, 79
Castoridae 78–81
Catacombs 68 ; see Edenvale
Caucasus 83, 115
cave deposits 41–2, 56, 58, 60–9, tab. 12 ; see localities
  disturbed 67
Cave Earth (Kent's Cavern) 62, 101, 104, tab. 12
Cervus see red deer
Chaline, J. 39
channels, buried 48–9
Cheddar 45
China 82, 87
Chinese Turkestan 121
Chudleigh (Fissure) 45, 70–1, 88, 90, 93, 104, 110, 117, 119, tab. 12
Citellus 75, 128 ; see *Spermophilus*
  erythrogenoides 75
  erythrogenys 75
  eversmanni 75
  nogaici 75
  (*Colobotis*) *superciliosus* 75, 77
  (*Urocitellus*) *polonicus* 75–6
    primigenius 75
  sp. 76
Clacton-on-sea 45, 49*, **52–3**, 78–80, 93, 101–2, 109, tab. 12, 123
Clactonian industry 50–1, 53
Clare, Co. 45 ; see Edenvale Caves
Clarke, Dr A. S. 130
classification 73–121
'clay pebbles' 47
Clethrionomys 92–4
  glareolus 37, 48, 52–3, 59–67, 70–2, **92–4**, tab. 12, 122–7, 129
  nageri 94
  sp. 53, 67, 92
Clevedon Cave 45, 66, 93, 111, 115–7, tab. 12, 126
Coelodonta see rhinoceros, woolly
Coffey Cave see Keshcorran
Colchester 45
Colobotis see *Spermophilus superciliosus*
Connaberry 45
Conodontes Boisvilletti 78
coombe rock 50, 59–60 ; see solifluxion deposits
Coope, G. R. 72, 113, 127–8, 130
Copford 45, 69, 78–9, tab. 12, 123
Coralline Crag 41, 96 (footnote)
Corbet, Dr G. B. 58, 72, 93, 110–1, 113, 115, 129
Corbicula Bed 54, 89, 92, 125
Cork, Co. 45 ; see localities
Corstorphine 45, 73, 88, 110, tab. 12
Covehithe 43, 45, 46*, 96, tab. 12
Cow Cave 45, 66, 115, tab. 12, 126
Cowside Cave No. 3 45, 70–1, 104, 110, 118, tab. 12
Cranbrook, Earl of 98
Crags 37, 41–2, 60 ; see Coralline, Icenian, Norwich, Red, Shelly and Weybourne Crags
Crayford 38, 45, 49*, 50, **54**, 60, 64, 66, 75, 92, 101–3, 111, 115, 117–8, tab. 12, 125–7
  Gravel 50
Creag nan Uamh Cave 45, **68**, 88, 110, 118, tab. 12
Cresswell 45 ; see Pin Hole Cave
Cricetidae 85–121
Cricetulus migratorius 87
Cricetus 48, 85–6, 127

cricetus 48, 63–6, **85–6**, tab. 12, 122, 124–6
major 86
runtonensis 86
runtonensis 86
songarus 37, 86–7
vulgaris Runtonensis 37, 85
Crocidura 64, 126
Crocuta see hyaena
Cromer 45, 46*, 78, 98, tab. 12
Cromer Forest Bed Series (Norfolk) 36–7, 40–1, 43, **46–8**, 74, 77, 79, 85, 94, 97–8, 105, tab. 12
Cromerian stage 40–1, 47, 60–2, 69, 78, 82–3, 85, 93, 96, 98, 101, 105–8, 114, 116, tab. 12
sensu stricto 47–8, 52, 61–2, 73, tab. 12, 122–3
Currant, A. P. 130
Cyrnaonyx 64, 126
Czechoslovakia 76, 86–7, 89, 96–9, 106, 109, 114, 116

Dama see fallow deer
deep-sea cores 40
deer see fallow, giant, red deer, reindeer, &c.
Denbighshire 45 ; see Lynx Cave
Denmark 113
Derbyshire 45 ; see localities
Devensian 41–2, 115, tab. 12, 127–8
Devon 45, 126 ; see localities
Diabroticus Schmerlingi 78
Dicerorhinus see rhinoceros, narrow-nosed
etruscus 61, 69
hemitoechus 56
kirchbergensis 56
Dicrostonyx 67, 69, 72–3, 87–90, 92, 111, 122–3, 127–9
gulielmi 87, 90
henseli 87, 90
hudsonius 90
simplicior 89
torquatus 37, 54, 59, 62–8, 70–2, **87–90**, 91–2, tab. 12, 125–6, 128
sp. 61, 87, 89, 124
Dierden's Pit 51 ; see Swanscombe
'Diluvium' (Tornewton Cave) 62–4, 66, 110, 117
Dipoides Lydekkeri 78
Diss 45 ; see Hoxne
distribution 73–121
Dnepr, river 121
Dog Holes Cave 45, 70–1, 77, 81, 88, 90, 93, 104, 109–10, 112–3, 117, 119, tab. 12
domestic animals 84
Domnitz 42
Doneraile 45
dormouse see *Muscardinus*, *Glis*
Dove Holes 60
Dowel Cave 45, 70–1, 74, 82–3, 88, 91, 93, 117, 119, tab. 12, 128
Dowel Dale 45 ; see Dowel Cave, Etches' Cave
Drepanosorex savini 101
Droitwich 45

Earl Sterndale 45
East Anglia 42, 46*, 98 ; see localities
deposits in 42–8, 69, 72
East Runton 38, 45, 46*, **47–8**, 78–80, 96, 98, tab. 12, 122
East Wickham 115
Easton Bavents 43, 45, 46*, 95, 98, tab. 12
Ebbsfleet 49–50, **59–60**
Eburonian 41, 43
Edenvale Caves 45, 68, 82, 88, tab. 12
Edinburgh 45 ; see Corstorphine
Edmonton 48, 49*, **59**
Edrom Parish 45 ; see Middlestots Bog
Eemian 40–2, 100
Elder Bush Cave 45, 70–1, 88, 91, 93, 104, 110, 117, tab. 12
elephant, straight-tusked 56–7
Elsterian 41, 61, 100
Ennis 45
Eocene 43
Eppelsheim 76
Equus see horse
mosbachensis 61
Erith 38, 45, 49*, 50, **54**, 75, 87, 89–90, 92, 115, 117, tab. 12, 125
Erkenbrechtsweiler 101
Erpfingen 1 and 2 101
Essex 45 ; see localities
Etches' Cave 45, 70–1, 83, 88, 91, 117, tab. 12, 128
Europe, continent of 36, 39, 43, 54, 74, 76–8, 80, 82–5, 87, 89, 92, 94, 97, 99, 105–8, 112–4, 116, 118, 120–2, 124, 126–8
Evans, P., half-cycles 40, 42, 127
Evotomys glareolus 92
harrisoni 92, 94
intermedius 95, 97–8
kennardi 92, 94
nageri 94
sp. 92, 94

Falconer, H. 37
fallow deer 56, 63

Felis see lynx
  gombaszoegensis 61
Felixstowe 45, 46*, 78
field-vole see Arvicola
Finland 112
fir cones, gnawed 74
Fisherton 45, 72, 76, 88, 115, 117, tab. 12
Fitch, Mr 96 (footnote)
Flandrian 41, 59, tab. 12
Flint bed 47
Flintshire 45 ; see Gwaenysgor Cave
Floodplain Terrace complex (Thames) **54**, 55–8
footprints 51
Forest Bed 42, 46*, 48, 53 ; see Cromer
Forest of Dean 115
fox, arctic 72
Fox Hole Cave 45, 70–1, 88, tab. 12, 128
France 74, 76, 78–9, 83, 87, 89, 95–9, 105, 109, 118, 120–1, 127

Geldeston 45, 46*, 98
geological background 40–2
Geological Society of London 40, 50, 55
Georgia 106, 116
Germany 76, 79, 87, 92, 96–9, 106, 109, 114, 116, 118, 124
giant beaver see *Trogontherium*
giant deer 68
Gippingian, Gipping cold stage 41, 56
glacial till 48
Glamorganshire 45 ; see Penard
Gliridae, glirids 43, 77–8
Glis glis 129
Gloucestershire see Alveston Fissure
glutton 63, 126
Glutton Stratum (Tornewton Cave) 63–6, 82, 85–6, 88–90, 92–3, 101–3, 110–1, 115, 117, 120, tab. 12, 125–6
  cold stage tab. 12, 125, 127
Gough's Cave 45, 66, 104, 110, 115, 117, tab. 12, 126
Grays Thurrock 38, 45, 49*, 50, 53–4, 57, 69, 80–1, 93, 101–3, 109, 111, 115, tab. 12, 125–6
Great Doward Cave 45, 70–1, 77, 81, 88, 91, 93, 110, 117, 119, tab. 12
Green, Rev. C. 48
Greenland 92
Gromov, I. M. 75, 77
ground squirrels see *Spermophilus*
Gulo see glutton, wolverine
Günz, Günz-Mindel 76
Gwaenysgor Cave 45, 70–1, 81, 88, 93, tab. 12

Hackney (Marshes) 45, 48, 49*, **59**, 88, tab. 12
hamster see *Cricetus*, *Allocricetus*
Happaway Cave 45, 70–1, 82–3, 93, 104, 110, 119, tab. 12
Happisburgh 45, 46*, **47–8**, tab. 12
Harborough Cave 45, 70–1, 91, tab. 12
Harkstead 45, 69, 72, 102–3, 110, 117, tab. 12, 125
harvest mouse see *Micromys*
Hay Wood Rockshelter 45, 70–1, 80, 118, tab. 12
Helmsley 45
Heppenloch 101
herbivores, large, trampling by 54
Herefordshire 45 ; see localities
Hertfordshire 45 ; see localities
Hessle 45, 69, 102, 104, tab. 12
High Wheeldon Hill 45 ; see Fox Hole Cave
hillwash 49 ; see Northfleet
Hinton, M. A. C. 35–40
  rodent faunas 40–1
hippopotamus, *Hippopotamus* 50, 56–9, 63, 67, 69, 86, 93, 102, 121, 125–7
history of rodent faunas 121–9
Hitchin 45, 69, 81, 93, tab. 12
Holland 43, 79, 83, 96–8, 116, 118
Holocene 41, 59–60, 62–4, 67, 70–3, 77, 80, 82–3, 93, 100, 102, 104, 113, tab. 12, 128–9
Holsteinian Interglacial 40–2, 79, 83, 95, 105, 124
Homo, hominids 51 ; see industries, man
Homotherium 62
  latidens 61
Hooker, J. J. 130
hornbeam 56
horse 56, 63, 72
Hoxne 42, 45, 69, 78–9, 81, 90, 92, 104, tab. 12, 123, 130
Hoxnian Interglacial 40–2, 52–3, 55–6, 65, 69, 78–80, 82, 92–3, 100–1, 104–8, 110, 116, tab. 12, **123**, 125
Hull see Kingston-upon-Hull
Hunas 101
Hundsheim 61, 101
Hungary 74, 76, 87, 89–90, 92, 95–8, 106, 109, 114, 116, 118, 120
Huntspill Cut 45, 73, 118, tab. 12 ; see Somerset
Hutton Cave 45, 58, 66–7, 86–7, 90, 93, tab. 12, 125–6
hyaena 62–3, 67, 69
Hyaena Stratum (Tornewton Cave) 63–6, 104, 110, 121, tab. 12, 125–6

Hypudaeus bucklandii 109
  spelaeus 103
Hystrix 43, 122

Iberian peninsula 99 ; see Spain
ice covering Britain 113
ice wedges 58
Icenian Crag 41, **43**, tab. 12, **122**
Ightham Fissures 37–8, 41, 45, 67, 76–7, 81, 83–4, 88, 91, 93–4, 101, 104, 110, 112–3, 117, 119, tab. 12
Ilford 45, 49–50, 53, 55–8, 60, 69, 80, 103, 109, tab. 12, 125–7
Inchnadamph 45, 67 ; see Creag nan Uamh Cave
Ingress Vale 51–2, 79, 81, 93, 100–2, tab. 12, 123–4 ; see Swanscombe
insects 36, 58, 72, 113, 127–8
Institute of Geological Sciences Museum 104
Ipswich 45, 72
Ipswich Museum 72, 97, 103–4, 110, 117
'Ipswichian' 57, 63, **67**, 69, 72, tab. 12, 125–7
Ipswichian stage (interglacial) 40–2, 50, 53–7, 82, 91, 124–5, 127
Ireland 42, 91, 129 ; see counties
  caves 68–9
  rodents in 121
  voles in 111–2
Iron Age 84 ; see Staple Howe
Isleworth 45, 48, 49*, **58**, 117, 119, tab. 12, 128
Italy 95, 97–8, 106, 114 ; see Val d'Arno

Jewell, Dr J. 130
Joint Mitnor Cave 45, 56, 67, 82, 93, 101–3, 110–1, tab. 12, 126
  interglacial tab. 12, 125–6

Kadzielnia 98
Kalkberg, Nagyhársanyberg 76
Kent 45, 50 ; see localities
Kent's Cavern 45, 60, **61**–**2**, 80, 83, 88, 91, 93, 101, 104, 107, 110, 117, 119, tab. 12, 122
Kerney, M. P. 51, 60, 63
Keshcorran Caves 45, 68, 82, 89, tab. 12
Kessingland 45, 46*, 78–9, 98, tab. 12
Kilgreany Cave 45, 68–9, 82, 84, 89, 111, tab. 12
King Arthur's Cave 45, 70–1, 88, 110, 117, 119, tab. 12
Kingston-upon-Hull 45 ; see Hessle
Kinlock 45
Kirkdale Cave 45, 56, 67, 81, 93, 104, 110, tab. 12
Koenigswald, W. von 36, 39, 64, 67, 69, 101, 129
  Mimomys–*Arvicola* faunal groups of 100–1, tab. 12, 124, 127
Koněprusy 101
Kopet-Dag 115
Kyson 45, 96

Lagurus 120–1, 127
  lagurus 63–6, **120**–**1**, tab. 12, 125–6
Lancashire 45 ; see Dog Holes Cave
Langwith Cave 45, 70–1, 74, 76, 82, 84, 88, 91, 93, 104, 110, 112, 117, 119, tab. 12
Last Glaciation 50, 54, 56, 58–60, 62–4, 67–72, 76, 82, 89–94, 102, 104, 111, 113, 118–21, 126, **127**–**8**, 129
Last Interglacial 40, 42, 50, 54–5, 56*, 59, 80, 89, 93, 102, 104
last interglacial 65, 78
Lea Valley 38, 41, 48–60, 49*, **58**–**9**, 128–9 ; see Nazeing, Ponders End, Water Hall Farm, &c.
Lebanon 115
lemming 54, 64, 67, 122, 127–9 ; see *Lemmus*, *Dicrostonyx*, *Lagurus*
Lemmus 37, 67–8, 90–2, 123–4, 127–9
  lemmus 54, 59, 62–6, 68, 70–1, **90**–**2**, tab. 12, 125–6, 128
  norvegicus 37, 90
  torquatus 87
  sp. 52, 61, 69, 90, 122–4
Levallois industries 49–50, 54
Levaton Cave 45, 67, 70–1, 82, 104, 110, 112, 117, 119, tab. 12, 128
Limerick, Co. 45 ; see Red Cellar Cave
lion 56, 63
Little Thurrock 50
localities with fossil rodents 42–73, 44–5*
Loch of Marlee 45, 73, 80, tab. 12
London 48, 58 ; see Hackney, Angel Road, &c.
Lough Gur 45
Lower Crayford Brickearth 50
Lower Loam (Swanscombe) 42, 52, 102, 108, 116, 123–4, 130
Lower Thames Valley province 48
Lowestoftian 41, 123
Ludhamian 41
lynx 68
Lynx Cave 45, 70–1, 82, 88, 110, 118, tab. 12

MacEnery, J. 62
Macoma balthica 43
Main Chamber see Tornewton Cave
Major, C. I. Forsyth 75
Male, H. C. 66
mammals other than rodents 56, 60, 72 ; see names
mammoth 50, 56–60, 62, 67–9, 72, 87, 129
Mammuthus 59 ; see mammoth
  primigenius 50
  trogontherii 50, 56
man, introductions to Britain by 83–4, 129
  remains, human 111
Marlow 45, 48, **58**, 113, 117, tab. 12, 129
mastodon 43
Mauer 61, 101
Mayhew, D. 130
Mediterranean 115
Medway, Upper Floodplain Terrace of 54
Megaceros see giant deer
melt-water deposits 59–60
Menapian 41
Mendips see Bleadon Cave, &c.
Merlin's Cave (=Wye Cave) 45, 70–1, 88, 91, 93, 101, 104, 110, 117, 119, tab. 12
Mesolithic 62, 128 ; see Star Carr, Thatcham
Micromys 66, 84
  minutus 65, **84**, tab. 12, 129
  sylvaticus 81
Microtinae 37–8, 43, 107, 111
Microtius (*Pitymys*) *arvalidens* 106
Microtus 69, 105, **107–8**, 108–20
  agrestis 37, 53–4, 58–9, 62–9, 72, 108, **109–12**, 113, 119, tab. 12, 125–7, 129
    neglectus 109
  of *agrestis* group 53
  agrestoides 109, 111
  anglicus 60, 118–20, 128
  arvalinus 48, 52, 61, **108–9**, 110–1, tab. 12, 122–4
  arvalis 58, 60, 72, 108–9, **112–3**, tab. 12, 127–8
  sp. (*arvalis*/*agrestis* group) 52, 60, 70–1, 108, **109**, 111
  corneri 109, 112–3
  eversmanni 120
  glareolus 92
  gregalis 58–60, 62–4, 66, 70–1, 107, 113, **118–20**, tab. 12, 126–8
  intermedius 102
  malei 114–6, 118
  nivalinus 114
  nivalis 37, 54, 59–60, 63–6, 72, **114–6**, tab. 12, 125–7
  nivaloides 48, **114**, tab. 12, 122–4
  oeconomus 37, 54, 58–9, 62–3, 65–8, 70–3, 108, 113, 115–6, **117–8**, tab. 12, 125–8
  orcadensis 112–3
  ratticepoides 48, 52, **116–7**, 118, tab. 12, 122–4
  ratticeps 68, 116–7
  subnivalis 114
  tianschanicus 120
  sp. 66, 69
  (*Pitymys*) *arvalidens* 105–6
    sp. 106
Middle East 100
Middle Terrace of Thames interglacial tab. 12, 125, 127
Middlesex 45 ; see Isleworth, Angel Road, Ponders End
Middlestots Bog 45, 73, 80, tab. 12
Midlothian 45 ; see Corstorphine
Mimomys 60, 95–100
  cantiana, cantianus 100, 102
  intermedius 98–9
  majori 98–9
  milleri 98–9
  newtoni 43, 47, **97–8**, tab. 12
  petenyi 97
  pliocaenicus 43, 47, **95–6**, tab. 12, 122
  polonicus 96
  reidi 43, **97**, tab. 12, 122
  savini 47–8, 52, 69, **98–9**, 100–1, 105, tab. 12, 122–4
    fauna tab. 12, 124 ; see *Arvicola*
  sp. 43
Mimomys–Arvicola lineage 36, 100, tab. 12, 129
Minchin Hole 45, 67, 103, 110, tab. 12,127, 129
Mindel 76
Miocene 43
Mitchell, Professor G. F. 130
mollusca 43, 51–2, 54, 56, 58, 63, 125
Monastirian, Late 40, 42, 50, 55
  Main 42, 50, 55
Mongolia 121
'monkey gravel' 48, 73, 122
Mosbach 61, 101, 122
multituberculate origin of rodents 38
Mundesley 45, 46*, 48, 75–6, 78–9, tab. 12, 122
  Arctic Bed tab. 12, **123**
Muridae, murids 43, 81–4
Murston 45, 88, tab. 12
Mus 84
  Abbotti 83
  Lewisi 83

  musculus 81, **84**, tab. 12, 129
  songarus 86
  sylvaticus 81
  sp. 81
Muscardinus 48, 77–8
  avellanarius 67, 70–1, **77–8**, tab. 12, 129
Myodes lemmus 90
  torquatus 87

narrow-skulled vole see *Microtus gregalis*
Nazeing 45, 48, 49*, **59**, 82, 88–9, 91, 93, 104, 118–9, tab. 12, 128
Neolithic 62, 83
Netherlands see Holland
Newhall Caves 68 ; see Edenvale
Newton, E. T. 37
Norfolk 38, 42, 45–6, 113 ; see localities
Nornour 45, 73, 118, tab. 12
North America 89–90, 92, 94, 118
Northfleet 45, 49*, 50, **59–60**, 93, 103, 110, tab. 12, 126
Norwich Crag 38, 41, 43, 46*, 47, 78, 95–8 ; see Icenian Crag
Norwich Museum 96 (footnote)

oak 56
Orkney Islands 109, 112–3
Orkney vole 112 ; see *Microtus arvalis*
Orsett Road 50, 53
Ostend (Norfolk) 45, 46*, 48, 53, 74, 101–2, 104, tab. 12, 123
  Forest Bed 47–8, 53, 74–5, 92, 122–3
otter, clawless 64, 126 ; see *Cyrnaonyx*
Otter Stratum (Tornewton Cave) 36, 64–5, 101–3, tab. 12, 126
Overstrand 45, 46*, 78, tab. 12
Owen, R. 37
owls 69, 112
ox, giant 56
Oxfordshire 45 ; see Sugworth

palaeobotany 39–40, 46–8, 55, 57, 59, 124–7 ; see pollen, plants
Palaeolithic 62–3, 66, 71
Palaeoloxodon antiquus 59 ; see elephant, straight-tusked
Palestine 105
Panthera see lion
Parapodemus coron. 101
Paston 45, 46*, 78, tab. 12
Pastonian (Forest Bed) 41, 43, **47–8**, 78–9, 96, 98, tab. 12, **122**
Peak District 36
Peakland Archaeological Society 67, 128, 130
Penard 45
Penkridge 89
Penultimate Glaciation 42
'penultimate' Glaciation 54, 56, 59, 64–5, 112, 114, 121, 125
Perpignan 78
Persia 105
Perthshire 45 ; see Loch of Marlee
Petersbuch 101
Phodopus 87
  sanfordi 86
  songorus 86–7
Picken's Hole 45, 70–1, 76, 117, 119, tab. 12, 128
Pin Hole Cave 45, 70–1, 76–7, 82–3, 88, 91, 93, 104, 110, 117, 119, tab. 12
pine 52, 56
pine vole see *Pitymys*
Pitymys 105–8
  arvalidens 105
  arvaloides 48, 52, 105, **106**, 107, tab. 12, 122–4
  gregaloides 48, 61–2, 105–6, **107**, tab. 12, 122–4
  sp. 69
plants 53, 58, 122, 127 ; see palaeobotany
Pleistocene 67, 74, 82–5, 87, 91–2, 112, 121–9, tab. 12
    generalized British sequence 41
  Lower 43, 60, 98, 121
  lower middle 80, 87, 89, 92, 94–5
  Upper 83
Pliocene 41, 43, 112, 122 ; 'Pliocene' 37, 40
Pliomys 95, 123
  episcopalis 61, **95**, 101, tab. 12, 122, 124
  lenki 101
Plumpstead 115
Plunkett Cave 68 ; see Keshcorran
Poland 76, 87, 89, 92, 96–8, 106, 116
pollen 36, 52, 55–6, 89, 128–9 ; see palaeobotany
  zonation of 'Ipswichian' sites 56*, 57–8
Ponders End 45, 48, 49*, 50, **59**, 88, tab. 12
post-Ipswichian 67
post-Pleistocene 68, 73 ; see Holocene
'preglacial' deposits 37
pre-'Ipswichian' 65–7
Prestatyn 45
Přezletice 101
Pyrenees 115

radiocarbon dating see carbon-14
Rangifer see reindeer
rat see *Rattus*
Rattus 84
  norvegicus **84**, tab. 12, 129
  rattus 67, 70–1, 74, **84**, tab. 12, 129
Red Cellar Cave 45, 68, 89, tab. 12
Red Crag 41, **43**, 46*, 78–80, 95, tab. 12, **122**
  basal nodule bed 43
red deer 56, 63, 67
reindeer 58, 63, 67–9, 72, 126
Reindeer Stratum (Tornewton Cave) 63–6, 88–9, 93, 101, 104, 110, 117, 119, tab. 12
Reuverian 41
rhinoceros 56, 59, 63
  narrow-nosed 63
  woolly 62, 67, 69, 72
Riss 42, 76, 100, 112, 121
Rodent Earth (Westbury) 60–1, 122, 124
rodent localities on British mainland tab. 12
Romania 92, 95–6, 109, 114, 116
Romano-British 71
root vole see *Microtus oeconomus*
Rowberrow Cavern 45, 70–1, 82, 88, 93, tab. 12
Russia 76, 87, 95–8, 106, 116

Saale 42, 50
Saalian 41
sabre-toothed cat 62 ; see *Homotherium*
Saint-Prest, Chartres 79
St Vallier, France 81
Salisbury 45
Salwarpe river 72
Sanford, W. A. 37
Savin collection 97
Scandinavia 92, 112–3 ; see Sweden, &c.
Scarborough 45
Scarcliffe 45 ; see Langwith Cave
Scilly Isles 45, 73, 118, tab. 12, 128 ; see Nornour
Sciuridae 73–7
Sciurus 73–4 ; see squirrel
  vulgaris 67, 70–1, **74**, tab. 12, 129
  whitei 48, **73–4**, tab. 12, 122, 124
    hungaricus 74
Scotland 73, 80, 128 ; see localities
  caves in 67–8, 118
Sealy, D. L. F. 130
Selsey 45, 69, 80, tab. 12
Settle 45
Seven Kings Station 55–6, 58
Severn river 72
Shell Cottages, Thorpe, Aldringham 96 (footnote)
Shelly Crag (East Runton) 38, 41, 47
shrew, white-toothed 64–5, 126 ; see *Crocidura*
Siberia 96–8, 105
Sieveking, G. de G. 60
Siliceous Group (Westbury) 60–1, 124
silver fir 56
Simons, J. 58, 66, 130
Singer, Dr R. 130
Sizewell 43, 45, 46*, 78, 95, 97, tab. 12
Sligo, Co. 45 ; see Keshcorran Caves
snow vole see *Microtus nivalis*
solifluxion deposits 59–60
Somerset 45 ; see localities
  caves 37
  Levels see Huntspill Cut
Sorex runtonensis 101
  savini 101
Soviet Union see Russia
Spain 87
Spencer, H. E. P. 96 (footnote), 130
Spermophilus 48, 54, **75**, 76
  altaicus 75–6
  citillus 76
  eversmanni 75–6
  erythrogenoides 37, 75–7
  erythrogenys 75
  sp. 75, 128
  (*Colobotis*) *superciliosus* 70–2, 75, **76–7**, tab. 12, 127
  (*Urocitellus*) *parryi* 76
    primigenius 54, **75–6**, 77, tab. 12, 125–7
    undulatus 76
squirrels 48, 74 ; see *Sciurus*
Staffordshire 45 ; see Elder Bush Cave
Stalagmite (Kent's Cavern) 62
Staple Howe 45, 72, 80, tab. 12
Star Carr 45, 73, 80, tab. 12, 128
Steinheim an der Murr 124
Stenocranius 120 ; see *Microtus gregalis*
steppe lemming see *Lemmus lemmus*
Stoke Tunnel Beds 45, 72, 103, tab. 12
Stuart, A. J. 39, 60, 69, 72, 81, 93, 102–4, 110, 117, 129
studies, history of 37–40
Stutton 45, 69, 72, 81, 101–3, 110, tab. 12, 125
Sudmer Berg 2 101
Suffolk 42–3, 45 ; see localities
Sugworth 45, 69, 98, tab. 12
Süssenborn 101
Sussex 45 ; see West Wittering, Selsey

Sutcliffe, Mrs A. J. 130
Sutherland 45 ; see Creag nan Uamh Cave
Sutton 43, 45, 46*, 79, tab. 12
Swaffley 45
Swanscombe 36, 38–9, 42, 45, 49*, 50, **51–2**, 53, 59, 78–81, 83, 90, 92–3, 100–2, 108–11, 115–6, tab. 12, 123–4
Swanton Morley 45, 69, 72, 81, 93, 101–3, tab. 12, 126
Sweden 78, 83
Switzerland 87, 89, 118, 120
Symond's Yat 45

Talpa europaea 101
  minor 101
Taplow terrace 55
Tarkö 61, 74, 101
terrace deposits 41–2, 48–60, tab. 12 ; see Thames
Thames 48–60, 49*, 62
  High Terrace 38, 41, 49, 51–3 ; see Swanscombe
  Lower **51–8**
  Middle Terraces 36, 38, 41, 49, 55, 57, 125
    early **53**
    interglacial see Middle Terrace of Thames interglacial
    late **54**, 125
  Middle Terrace/Floodplain Terrace problem **55–8**
  Third Terrace 38, 41, 54, 55
  Upper **58**
  Upper Floodplain Terrace 55–8
Thatcham 45, 73, 80, 104, tab. 12
Thorpe, Aldeburgh, Suffolk 96 (footnote)
Thorpe, Norfolk 43, 45, 46*, 78, 96 (incl. footnote), tab. 12
Thorpeness 96 (footnote)
Thurnian 41, 43
Tiglian 41, 43, 78, 83, 96–8, 122
tooth-enamel 81, 100
Torbryan 45
Tornewton Cave 36, 45, **62–5**, 66–7, 81, 84–90, 92–3, 101–4, 110–1, 115, 117, 119–21, tab. 12, 125–6
Torquay 45
Trafalgar Square 55–8, 127
Treacher collection 58, 113
Trimingham 43, 45, 46*, 97, tab. 12
Trogontherium boisvilletti 43, 47–8, 52–3, 69, **78–9**, tab. 12, 122–4
  cuvieri 37, 53, 78–9
  minus 37, 43, **78**, 122
  sp. 78
Turner, C. 54

Ukraine 74, 76, 114
Uphall Estate 109
Uphill Cave 45, 70–1, 91, 119, tab. 12
Upnor 45, 49*, 54, 80, tab. 12
Upper Freshwater Bed (West Runton) 38, 41, 48, 52, 73, 81, 83, 85, 93, 97–101, 105, 107–8, 114, 116, 124
Upper Langwith 45
Upper Rodent Stratum (Tornewton Cave) 64–6
Uppony 101
Upton Warren 45, 69, 72, 88, tab. 12, 128
  interstadial complex 128
Urals 83
Urocitellus 125 ; see *Spermophilus primigenius*
Ursus see bear
  deningeri 61

Val d'Arno, Italy 80–1, 96
Vejlby I and II mild stages (Denmark) 40, 42
Villafranchian 41, 43, 47, 76, 81, 92, 95–6, 122
Viscount Melville Sound 92
Voigtstedt 101
voles 38–9, 47, 51, 69 ; see *Arvicola*, *Mimomys*, *Microtus*
  in Ireland ? 69, 129

Waalian 41, 43
Waechter, J. d'A. 51, 130
Wales, south 113
Waltonian 41
Warthe 42
Warton Crag 45 ; see Dog Holes Cave
Water Hall Farm (Pit) 45, 48, 49*, **58–9**, 110, 115, 117, tab. 12, 126, 130
Waterford, Co. 45 ; see localities
water-rat, water-vole see *Arvicola*
Weichsel 42
Weichselian 41
West, R. G. 47, 130
West Runton 38, 41, 45, 46*, 47–8, 52, 60–1, 73, 78–9, 81, 83, 85, 93, 97–100, 105–8, 114, 116, tab. 12, 122–4
West Thurrock 50

West Wittering 45, 93, tab. 12
Westbury-sub-Mendip (fissure) 36, 45, **60–1**, 80–1, 87, 89–90, 92–3, 95, 101–2, 105, 107–8, 121, tab. 12, 122–4, 129
Westbury stage 108, tab. 12, **122**, 123
Wetton 45
Weybourne Crag 38, 41, 43, 46*, 47, 95–7; see Icenian Crag
Whitchurch 45
White Sea 120
Whitechurch 45
Willment's Gravel Pit 58, 128, 130
Wilson, Mrs G. 130
Wiltshire 45; see Fisherton
Wintringham 45
wolf 62–3
Wolff, R. G. 69, 81, 90, 104, 130
Wolstonian stage 40–2, 50, 52, 54–5, 124–5
wolverine 126; see glutton
wood mouse see *Apodemus sylvaticus*
Woodbridge 43, 45, 46*, 78–9, tab. 12
Worcestershire 45; see localities
Wretton 91
Würm 42, 76, 121
Wye Cave see Merlin's Cave

Xenocyon lycaonoides 61

yellow-necked mouse see *Apodemus flavicollis*
Yorkshire 45; see localities
Yugoslavia 98, 106, 109, 114

A. J. Sutcliffe, Ph.D.
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

K. Kowalski
Institute of Systematic and Experimental Zoology
Polish Academy of Sciences
Krakow
Poland

Accepted for publication 28 October 1975

A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. Cox, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. OUT OF PRINT.
2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £11.
3. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £8.20.
3. Appendix. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.
4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 16 Text-figures. 1968. OUT OF PRINT.
5. Rhodes, F. H. T., Austin, R. L. & Druce, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 313; 31 Plates; 92 Text-figures. 1969. £13.10.
6. Childs, A. Upper Jurassic Rhynchonellid Brachiopods from Northwestern Europe. Pp. 119; 12 Plates; 40 Text-figures. 1969. £5.25.
7. Goody, P. C. The relationships of certain Upper Cretaceous Teleosts with special reference to the Myctophoids. Pp. 255; 102 Text-figures. 1969. £7.70.
8. Owen, H. G. Middle Albian Stratigraphy in the Anglo-Paris Basin. Pp. 164; 3 Plates; 52 Text-figures. 1971. £7.20.
9. Siddiqui, Q. A. Early Tertiary Ostracoda of the family Trachyleberididae from West Pakistan. Pp. 98; 42 Plates; 7 Text-figures. 1971. £9.60.
10. Forey, P. L. A revision of the elopiform fishes, fossil and Recent. Pp. 222; 92 Text-figures. 1973. £11.35.
11. Williams, A. Ordovician Brachiopoda from the Shelve District, Shropshire. Pp. 163; 28 Plates; 11 Text-figures; 110 Tables. 1974. £12.80.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

SBM. 0

BRITISH MUSEUM GENERAL 24 SEP 1976 LIBRARY NATURAL HISTORY

A MONOGRAPH ON FOSSIL BEES (HYMENOPTERA: APOIDEA)

F. E. ZEUNER

AND

F. J. MANNING

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 3
LONDON: 1976

BRITISH MUSEUM
GENERAL
7 SEP 1976
LIBRARY
NATURAL HISTORY

A MONOGRAPH ON FOSSIL BEES (HYMENOPTERA : APOIDEA)

BY
THE LATE FREDERICK EVERARD ZEUNER
AND
THE LATE FRANCIS JOSEPH MANNING
EDITED WITH AN APPENDIX
BY
SAMUEL FRANCIS MORRIS
British Museum (Natural History)

Pp. 149–268 ; 4 *Plates*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 3
LONDON : 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 27, *No.* 3, *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007–1471

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 23 *September,* 1976 *Price* £8.80

A MONOGRAPH ON FOSSIL BEES (HYMENOPTERA: APOIDEA)

By THE LATE F. E. ZEUNER AND THE LATE F. J. MANNING

CONTENTS

		Page
	SYNOPSIS	155
I.	INTRODUCTION	155
II.	TERMINOLOGY AND CLASSIFICATION	156
III.	MATERIAL STUDIED	158
IV.	SYSTEMATIC PALAEONTOLOGY: SYNONOMIC LIST OF FOSSIL BEES (EXCLUDING APIDAE)	161
	Superfamily APOIDEA Ashmead	161
	Family COLLETIDAE Bingham	161
	Family HALICTIDAE Ashmead	162
	Subfamily HALICTINAE Ashmead	162
	Genus *Cyrtapis* Cockerell	163
	Cyrtapis anomalus Cockerell	163
	Genus *Halictus* Latreille	163
	Halictus ruissatelensis Timon-David	164
	Halictus florissantellus Cockerell	164
	Halictus miocenicus Cockerell	164
	Halictus scudderiellus Cockerell	164
	Halictus schemppi (Armbruster)	164
	Family ANDRENIDAE Latreille	165
	Subfamily ANDRENINAE Latreille	165
	Genus *Andrena* Fabricius	165
	Andrena wrisleyi Salt	166
	Andrena clavula Cockerell	166
	Andrena grandipes Cockerell	166
	Andrena hypolitha Cockerell	166
	Andrena lagopus Latreille	167
	Andrena percontusa Cockerell	167
	Andrena sepulta Cockerell	167
	Andrena primaeva Cockerell	167
	Andrena spp. indet.	168
	Genus *Lithandrena* Cockerell	169
	Lithandrena saxorum Cockerell	169
	Genus *Pelandrena* Cockerell	169
	Pelandrena reducta Cockerell	170
	Subfamily PANURGINAE Leach	170
	Genus *Libellulapis* Cockerell	170
	Libellulapis antiquorum Cockerell	170
	Libellulapis wilmattae Cockerell	171
	Family Andrenidae *incertae sedis*	171
	Andrenidae gen. et sp. indet.	171
	Family MELITTIDAE Dumeril	171
	Subfamily CTENOPLECTRINAE Cockerell	172
	Genus *Ctenoplectrella* Cockerell	172
	Ctenoplectrella dentata Salt	172
	Ctenoplectrella viridiceps Cockerell	173

Page
Genus *Glyptapis* Cockerell 173
Glyptapis fuscula Cockerell 173
Glyptapis mirabilis Cockerell 173
Glyptapis neglecta Salt 174
Glyptapis reducta Cockerell 174
Glyptapis reticulata Cockerell 174
Subfamily MELITTINAE Dumeril 174
Genus *Melitta* Kirby 175
Melitta willardi Cockerell 175
Family Melittidae *incertae sedis*. 175
Dasypoda (s.l.) sp. indet. 175
Family MEGACHILIDAE Latreille 175
Subfamily LITHURGINAE Newman 176
Genus *Lithurge* Latreille 176
Lithurge adamitica (Heer) 176
Subfamily MEGACHILINAE Latreille 178
Tribe ANTHIDIINI Michener 178
Genus *Anthidium* Fabricius 178
Anthidium mortuum (Meunier) 178
Anthidium exhumatum Cockerell 179
Anthidium scudderi Cockerell 179
Genus *Dianthidium* Cockerell 179
Dianthidium tertiarium Cockerell 180
Genus *Lithanthidium* Cockerell 180
Lithanthidium pertriste Cockerell 180
Tribe MEGACHILINI Latreille 180
Genus *Heriades* Spinola 180
Heriades bowditchi Cockerell 181
Heriades halictinus Cockerell 181
Heriades laminarum Cockerell 181
Heriades mersatus Cockerell 181
Heriades mildredae Cockerell 181
Heriades priscus Cockerell 182
Heriades saxosus Cockerell 182
Genus *Megachile* Latreille 182
Megachile amaguensis Cockerell 182
Megachile praedicta Cockerell 183
Megachile sp. indet. 183
Genus *Osmia* Panzer 183
Osmia carbonum Heyden 184
Osmia antiqua Heer 184
Osmia nigra sp. nov. 185
Osmia sp. indet. 186
Family Megachilidae *incertae sedis* 186
'Apiaria' dubia Germar 186
Megachilidae gen. et sp. indet. 186
Family ANTHOPHORIDAE Dahlbom 187
Subfamily XYLOCOPINAE Latreille 187
Tribe CERATININI Latreille 188
Genus *Ceratina* Latreille 188
Ceratina disrupta Cockerell 188
Tribe XYLOCOPINI Latreille 188
Genus *Xylocopa* Latreille 189

Page
Xylocopa friesei Statz 189
Xylocopa hydrobiae Zeuner 189
Xylocopa jurinei (Heer) 189
Xylocopa senilis Heer 190
Subfamily ANTHOPHORINAE Dahlbom 192
Tribe EUCERINI Latreille 192
Genus *Tetralonia* Spinola 193
Tetralonia berlandi Théobald 193
Tribe ANTHOPHORINI Dahlbom 193
Genus *Anthophora* Latreille 194
Anthophora melfordi Cockerell 194
Genus *Anthophorites* Heer 194
Anthophorites gaudryi Oustalet 195
Anthophorites thoracica Heer 195
Anthophorites longaeva Heer 195
Anthophorites mellona Heer 196
Anthophorites titania Heer 197
Anthophorites tonsa Heer 198
Anthophorites veterana Heer 198
Tribe MELECTINI Westwood 199
Genus *Promelecta* Cockerell 199
Promelecta brevipennis Cockerell 199
Family Anthophoridae *incertae sedis* 200
'Anthophora' effossa Heyden 200
Anthophoridae gen. et sp. indet. 200
Superfamily Apoidea (except Apidae) *incertae sedis* . . . 201
Apoidea gen. et sp. indet. 201
Fossils erroneously classified as Apoidea (excluding Apidae) . 202
'Formicinae' 202
Polistes kirbyanus Cockerell 202
Larval Chambers 203
'Genus' *Celliforma* Brown 203
Celliforma favosites Brown 203
Celliforma spirifer Brown 203
Celliforma germanica Brown 204
Celliforma nuda Brown 204
Celliforma bedfordi sp. nov. 204
Celliforma septata sp. nov. 205
Celliforma sp. indet. 205
'Genus' *Uruguay* Roselli 205
Uruguay auroranormai Roselli 205
V. SYSTEMATIC DESCRIPTIONS OF FOSSIL APIDAE 206
Family APIDAE Latreille 206
Chalcobombus group 206
Genus *Chalcobombus* Cockerell 206
Chalcobombus hirsutus Cockerell 207
Chalcobombus humilis Cockerell 208
Chalcobombus martialis Cockerell 208
Tribe BOMBINI Latreille 209
Genus *Bombus* Latreille 209
Bombus crassipes Novak 209
Bombus abavus Heer 210
Bombus florissantensis (Cockerell) 212

Page
Bombus proavus Cockerell 212
Tribe Meliponini Handlirsch 213
Genus *Sophrobombus* Cockerell 213
Sophrobombus fatalis Cockerell 214
Genus *Trigona* Jurine 216
Subgenus *Trigona* Jurine 217
Trigona (*Trigona*) *erythra* Schletterer . . . 217
Subgenus *Hypotrigona* Cockerell 218
Trigona (*Hypotrigona*) *gribodoi* Magretti . . 218
Subgenus *Tetragona* Lepeletier & Serville . . . 221
Trigona (*Tetragona*) *succini* (Tosi) . . . 221
Trigona (*Tetragona*) *iridipennis* Smith . . . 222
Subgenus indet. 224
Trigona sicula (Tosi) 224
Tribe Apini Latreille 225
Genus *Electrapis* Cockerell 225
Subgenus *Electrapis* Cockerell 227
Electrapis (*Electrapis*) *apoides* Manning . . . 227
Electrapis (*Electrapis*) *meliponoides* (Buttel-Reepen) 229
Electrapis (*Electrapis*) *tornquisti* Cockerell . . 231
Subgenus *Protobombus* Cockerell 231
Electrapis (*Protobombus*) *indecisus* (Cockerell) . . 232
Electrapis (*Protobombus*) *tristellus* (Cockerell) . . 233
Subgenus *Roussyana* Manning 233
Electrapis (*Roussyana*) *palmnickenensis* (Roussy) . 233
Electrapis (*Roussyana*) *proava* (Menge) . . . 236
Genus *Apis* Linnaeus 239
Subgenus *Synapis* Cockerell 240
Apis (*Synapis*) *cuenoti* Théobald 240
Apis (*Synapis*) *henshawi* Cockerell . . . 240
Apis (*Synapis*) *henshawi dormiens* subsp. nov. . 241
Apis (*Synapis*) *henshawi henshawi* Cockerell . 242
Apis (*Synapis*) *henshawi kaschkei* (Statz) . . 243
Subgenus *Apis* Linnaeus. 243
Apis (*Apis*) *armbrusteri* Zeuner 244
Apis (*Apis*) *armbrusteri armbrusteri* Zeuner. . 245
Apis (*Apis*) *armbrusteri scharmanni* (Armbruster) 246
Apis (*Apis*) *armbrusteri scheeri* (Armbruster) . 247
Apis (*Apis*) *armbrusteri scheuthlei* (Armbruster) . 247
Apis (*Apis*) *melisuga* (Handlirsch) 248
Apis (*Apis*) *mellifera* Linnaeus 249
Family Apidae *incertae sedis* 250
'Apis' aquitaniensis de Rilly 250
'Apis' dormitans Heyden 251
'Apis' styriaca Pongrácz 251
'Bombus' carbonarius Menge. 252
'Bombus' muscorum Roussy 252
'Bombus' pusillus Menge 252
'Bombus' antiquus Heyden 252
'Bombus' grandaevus Heer 253
'Bombusoides' mengei Motschulsky 253
Apidae gen. et sp. indet. 254

		Page
	NOT APIDAE	255
	Lithoblatta lithophila (Germar)	255
VI.	APPENDIX, *by* S. F. Morris	255
	Colletidae gen. et sp. indet.	255
	Ctenoplectrella splendens Kelner-Pillault	255
	Anthiidini gen. et sp. indet.	256
	Osmia sp.	256
	Apoidea (? Anthophorinae) sp.	256
	Probombus hirsutus Piton (ms)	256
	Trigona (*Hypotrigona*) *eocenica* Kelner-Pillault	256
	Trigona (*Hypotrigona*) *dominicana* Wille & Chandler	256
	Trigona (*Nogueirapis*) *silacea* Wille	257
	Electrapis minuta Kelner-Pillault	257
	Apis catanensis Roussy	257
	? Apoidea sp.	257
	Not Apoidea	257
VII.	ACKNOWLEDGEMENTS	257
VIII.	REFERENCES	258
IX.	INDEX	264

SYNOPSIS

The status of 128 species of fossil bees and nests are reviewed, 19 of which are left under open nomenclature. Four species are removed from the Apoidea. A new species *Osmia nigra* sp. nov. and subspecies *Apis* (*Synapis*) *henshawi dormiens* subsp. nov. of bees, and two new 'species' of bees' nests *Celliforma bedfordi* sp. nov. and *Celliforma septata* sp. nov., are described. An appendix covering the years 1960–74 has been added.

I. INTRODUCTION

by S. F. Morris

UNTIL 1949, Professor Zeuner and Dr Manning had each been independently working on monographs of fossil bees, and until that time they were unaware of each other's work. But in 1949 they met and agreed to combine their efforts into a joint monograph. This collaboration continued until the death of Professor Zeuner in 1963, followed by the death of Dr Manning in 1966.

The major part of the present work was already finished by 1959, but the authors seemed to have had problems which prevented them completing it. The monograph lacks a projected part which was to have dealt with the evolution of the bees, but there are no extant manuscript notes for this. Certainly in 1964 Dr Manning was investigating a sphecid wasp from the Jurassic of Lerida Province, Spain, which he thought might be (or be closely related to) the ancestor of the bees. No written material of this work is extant either.

Entries to the main body of the monograph ceased about 1959, so the editor has added an Appendix (p. 255) containing fossil bee references since that date, and a few earlier ones that the authors had missed which have since come to his notice. A few minor alterations to the body of the text have been made in order to bring it into line with modern taxonomic work.

Although the monograph is intended to be a world-wide catalogue of fossil bees, the authors did not have the opportunity to re-examine the American species, so that the taxonomic aspects of these are not treated in as great a depth as are the European ones. In the main the authors have had to rely on the original authors' descriptions and figures for the American species except where the specimens were deposited in a European institution.

Since this work was carried out some years ago, references to various institutions may be badly out-of-date, especially the war-damaged European museums. It has not, however, been the principle of the editor to undertake any significant alteration to the typescript as it stood. The taxonomic work as published is in two parts, the Apoidea excluding the Apidae (Section IV), and the Apidae (Section V). The division appears to have been made in this way because it most nearly represents the division between the New World and Old World fossil bees, and allows for different treatments of the two parts.

The textfigures and plates had been made but have disappeared and were not amongst the effects of either of the authors. Fortunately the British Museum (Natural History) still retained negatives of many of the photographs and these have been reprinted for the plates. No attempt has been made to redraw the missing textfigures, since it is not known what they were or what they were intended to show. New photographs have been taken of specimens that are deposited in the British Museum (Natural History).

Professor Zeuner was a Research Associate of the British Museum (Natural History), which position he had held since 1934 until his death. His obituary was published in 1963 in *Nature, Lond.* **200** : 1263. An obituary for Dr Manning appeared in 1966 in *Proc. R. ent. Soc. Lond.* (C) **31** : 62.

II. TERMINOLOGY AND CLASSIFICATION

The study of fossil bees, like that of any other group, requires a reasonably satisfactory system of classification. It may not always express fundamental relationships, but it must be consistent with the morphological evidence available. Michener (1944, 1965) attempted a revision of the families, subfamilies and tribes of bees of the world and of the North American genera in particular – a formidable task. From its very magnitude it was clear that the result would not completely satisfy the author himself, nor could it entirely agree with all the considered opinions of all bee taxonomists. His groups, however, well express relationships that have for long been obscure, and the inclusion of the bee families in the Sphecoidea has much to recommend itself. For these reasons, Michener's classification of the bees has been adopted in the present monograph.

In the past, the lack of uniformity of the use of a terminology for their morphology has been a serious difficulty in the study of bees. Fortunately Snodgrass (1935) and more recently Michener (particularly 1944) have devoted considerable time and effort to clarifying this unhappy state of affairs, and we have taken advantage of the results of the labours of these authors. Moreover, the often excellent preservation of the fossil forms makes it necessary to treat them as if they were Recent specimens, and to make detailed reference to morphological characters. This is particularly true, for instance, of specimens from Rott which show such intimate features as wax mirrors and parts of the alimentary canal. A modern terminology, therefore, is imperative. The terms used in this monograph for the structural features of the hind legs are defined later.

With regard to wing venation the system of Ross (1936) has been adopted, together with the use of the following terms: submarginal cells, submarginal cross veins (i.e. 2nd abscissa Rs, 1st r-m, 2nd r-m) and recurrent veins (1st m-cu and 2nd m-cu). The term 'intercubitus' has become obsolete with the rejection of the use of the term 'cubital cells' for the submarginal cells. The very convenient term 'basal vein', however, is retained for the free (i.e. not fused) sections of both M and Rs, which run from opposite directions towards each other before they unite to form a vein Rs + M.

In addition, the term 'bomboid' is frequently used in the discussions that follow. This is not synonymous with '*Bombus*-like' but is intended to suggest that the characters in question are merely reminiscent of those of the tribe Bombini. Bomboid forms need not be closely related to Recent Bombini, though perhaps derived from either the ancestral form of the Bombini or, just as probably, from the ancestral form from which both the Bombini and the other Apidae arose. The last-mentioned possibility might imply that the Apini and Meliponini are not descended from the Bombini. The term 'apoid' is used in a somewhat similar sense in its appropriate context.

Other terms, important because of their evolutionary significance, are those defining certain structures of the hind legs. The most essential are the following: (1) tibial comb, (2) tibial rake, or pollen rake, (3) tibial spur, (4) auricle, (5) depstum, and (6) basitarsal brush.

The TIBIAL COMB[1] is a structure much like a comb, situated on the *outer* side of the apex of the tibia, above the tibio-basitarsal joint. It consists of strong hairs, fused at the base, which usually project backwards and downwards.

The TIBIAL RAKE is the dense row of spines or spine-like hairs along the apical edge of the *inner* side of the tibia.

The TIBIAL SPURS are the two large and sharp spines which are jointed to the tibia. They protrude from the lower apical margin of the hind tibia. In the normal walking position, with the hind legs slightly turned outwards, they have to be looked for underneath in a seemingly forward position. If two spurs are present they are distinguished as the inner and outer hind tibial spurs. The inner one is often serrate. If only one is present, it may be either the outer or the inner, and one can be distinguished from the other by its position relative to the apical rim of the tibia and by the presence or absence of serration, sometimes expanded into a comb-like structure. Thus a single spur with one edge serrate, occupying a relatively deep, inner position, is assumed to be the inner tibial spur, and a straight spur without serration, occupying a more marginal position, is assumed to be the outer.

---

[1] The honey bee and the bumble bee lack this comb, but nevertheless have one or two hairs situated on the outer apical face of the corbicula. The derivation of these hairs is not known. Their position, however, precludes them from being direct derivatives of the tibial comb. They have not been noticed in fossil Apinae but might easily have been overlooked. They are used for stabilizing the load of pollen.

The AURICLE is the more or less broadened upper tip of the basitarsus which lies below the distal end of the tibia. It is like a projecting lip neatly fitting the complementary shape of the tibial apex, and in Recent *Apis* it is set with minute stud-like eminences. Often both the lip and tibial apex have been jointly termed the auricle, a practice not followed here.

DEPSTUM is a term used for an angularity of the basitarsus which is sometimes present where no true auricle is developed. This is a primitive condition, although some bees (e.g. Meliponini) do not even have a depstum in the modern species.

Lastly, the term BASITARSAL BRUSH is reserved for the neatly aligned rows of bristles present on the inner surface of the basitarsus of the Apini. It is not used for the haphazard arrangement of hairs found in other groups.

III. MATERIAL STUDIED

For the study of the fossil Apidae a fair amount of material was available in the British Museum (Natural History), the total number of specimens being 52. The Meliponini, for instance, lacked only the specimens from the Sicilian amber which had been well described and illustrated by Tosi as long ago as 1896. The Apini lacked only representatives of the bees from Randecker Maar, mainly in the Armbruster Collection, but these were examined by one of the authors. It was only in the Bombini that the Museum collection really lacked material, due to the extreme paucity of the fossils of this tribe. Fortunately the most important representative, *Bombus proavus* Cockerell, has been well photographed and described (1931).

Furthermore, during 1950 and again in 1951, both authors travelled independently on the European continent studying fossil Apidae. Collections in Holland, Germany and Switzerland were examined. One of us had carried on this study of continental material for a number of years before it was decided to continue the work jointly.

Whilst fossil Apoidea are plentiful in Europe, the absence of material belonging to families of bees other than the Apidae is disappointing. This material is chiefly in American museums and must await discussion by someone from there. Our attempts to obtain information or specimens from the relevant museums remained, unfortunately, without significant success. Below are given the names of the more important collections of fossil Apidae or museums where such material is to be found.

ARMBRUSTER COLLECTION. In the sediments of a small volcanic lake at Randeck, Württemberg, honey bees have been found by numerous collectors. Possibly the oldest known specimens are those in the Oscar Fraas Collection, Stuttgart. In 1926, however, William Scheuthle of Goeppingen began his search for fossil honey bees, and just over a year and a half later was assisted by Professor L. Armbruster. When the former died in November 1928, substantial discoveries had already been made and the collection eventually passed entirely into the possession of Professor

Armbruster. Other collections believed to contain Randecker Maar honey bees are those of Eduard Scheer of Goeppingen, Bernard Hauff of Holzmaden, Karl Schempp of Brucken, and Pfarrer Hermann of Holzmaden.

BAUCKHORN COLLECTION. See Siegburg an der Lahn (p. 160).

BURSEY COLLECTION. The collection of amber fossils formerly belonging to Mr Maurice Bursey of Surbiton, Surrey, now in the Muséum National d'Histoire Naturelle, Paris, contains the important specimen *E.* (*Electrapis*) *apoides* Manning (p. 227).

COCKERELL COLLECTION. The late Professor T. D. A. Cockerell of the University of Colorado collected and studied fossil bees. His main collections were made from the Miocene lake deposits of Florissant, Colorado, particularly during the expedition of 1906–7, when he was accompanied by his wife, Dr W. M. Wheeler and Mr S. A. Rohwer. His collections of fossil bees appear to have been few, and are now in the University of Colorado Museum, Boulder, Colorado, and the American Museum of Natural History. Although more of his other fossil insects are in the British Museum (Natural History), the only bee from his collection to be found there is *Anthophora melfordi* Cockerell.

DANZIG, Poland: Westpreussisches Provinzial-Museum. Many Baltic amber specimens were to be found here, but the whereabouts of the collection is not known at the present time.

KARLSRUHE i.B., Germany: Badische Landessammlung für Naturkunde, Erbprinzenstrasse 13. Contains some of the Oeningen and Radoboj material described by Oswald Heer. The building itself is in ruins, but the cellars are still packed with material and it is possible, therefore, that some further types, at present untraceable, will be found.

KLEBS COLLECTION. From time to time Baltic amber specimens were formerly sold to private collectors and to museums, and it appears that this dispersal was made by the firm of Messrs Stantien & Becker, who traded the amber and who later were taken over by the Prussian State Amber Works. Messrs Stantien & Becker, in their day, placed the amber fossils in charge of Richard Klebs (1850–1911) who was, in later years, state geologist to the Prussian Geological Survey. A set of 346 specimens, including the holotype of *E.* (*Roussyana*) *proava* Menge (p. 236), was acquired by the British Museum (Natural History) from Messrs Stantien & Becker in 1892, but since the specimens bear labels marked 'R. Klebs, Museum Stantien & Becker', this collection has usually gone under the name of 'Klebs Collection'. (See also p. 238.)

KOENIGSBERG, East Prussia, U.S.S.R.: Geologisch-Paläontologisches Institut und Museum der Universität. The most important types and described specimens of Baltic amber bees were included in this collection. They are now housed in the Museum of the Humboldt University, Berlin.

MAINZ (Rhein), Germany: Naturhistorisches Museum der Stadt Mainz. Contains a large collection of insect remains from the *Hydrobia*-limestone of the district around Mainz.

LONDON, British Museum (Natural History). See under Klebs Collection, Swinhoe, R. C. J., Luke Thomas Collection and Krantz, F. This collection includes some 52 specimens, including the types of Heyden (1862), and others from the Baltic amber, Rott am Siebengebirge, Florissant, Böttingen, East African copal, Burmese copal and South Australia.

MARSEILLE, France : Musée. According to Armbruster (1938) and Roussy (personal communication), the specimen of *'Apis' aquitaniensis* de Rilly (No. 5979) (p. 250) is in this collection, and Meunier (1915) states that a specimen of *Anthophorites mellona* Heer (p. 196) is also in it. No confirmation, however, can be obtained after repeated enquiries. The Marseille Museum is rich in fossil insects from the Tertiary of southern France.

ROUSSY COLLECTION. This is the private collection of Monsieur Louis Roussy, Aigle, Switzerland, and contains mainly Baltic amber specimens, including *Electrapis* (*Roussyana*) *palmnickenensis* (Roussy), p. 233.

SCHEELE COLLECTION. This important collection of several thousand specimens of Baltic amber has been purchased by the Geologisches Staatsinstitut, Hamburg. Several important specimens of *Electrapis* are included.

SIEGBURG AN DER LAHN, Germany : Städtisches Heimatmuseum. This museum contains the valuable collection of fossil insects made by Hugo Bauckhorn. It is particularly rich in specimens from Rott, previously studied by Meunier and Statz.

STATZ COLLECTION. Fossil insects from Rott am Siebengebirge have been collected for over a century and are to be found in many museums and institutions. The collection made by the late Georg Statz of Cologne has become famous for the number and quality of its specimens. Moreover, Statz described and figured large numbers of his specimens. His collection includes several dozen fossil bees some of which have been well described and play an important role in the reconstruction of the phylogeny of the group. It is much to be regretted that this collection has been removed to Algiers, where it is in the hands of the collector's daughter.

STUTTGART, Germany : Württembergische Naturaliensammlung. This collection includes the material from Boettingen Swabian Alb, a locality situated not far from Randeck. One of us, while studying the fauna of this area, discovered a fossil swarm of honey bees, and casts were made of some of the bodies comprising it. Unfortunately it is believed that the original specimens were destroyed during the war, but the casts are still preserved in the British Museum (Natural History).

SWINHOE COLLECTION. Specimens of insect inclusions in the dark and pale varieties of Burmese amber from the Hukong Valley were collected by R. C. J. Swinhoe and presented to Professor T. D. A. Cockerell. Some were later presented by Cockerell to the British Museum (Natural History). Only the pale Burmese amber is known to contain bees.

TIMON-DAVID COLLECTION, Marseille. This collection consists of fossil insects from Camoins (Bassin de Marseille) and other French localities, and includes the fossil bee *Halictus ruissatelensis* Timon-David (p. 164).

LUKE THOMAS COLLECTION. A number of specimens of fossil bees are from East African copal. These, and other insects, have been presented to the British Museum (Natural History) at various times by individual donors. The Luke Thomas Collection contains twelve pieces of copal including fossil bees belonging to the Meliponini. They were presented to the British Museum (Natural History) in 1945 by Col. H. Burrows. All are from the east coast of the mainland of Africa, facing Zanzibar.

WASHINGTON, D.C., U.S.A.: United States National Museum; Smithsonian Institution. Contains part of the collection, mainly from Florissant, described by Professor T. D. A. Cockerell.

WICKHAM COLLECTION. The late Professor H. F. Wickham collected material from the Miocene shales of Florissant, Colorado, particularly at Wilson Ranch. This collection, which contains *Andrena percontusa* Cockerell (p. 167), is in Yale University.

ZÜRICH, Switzerland: Geologisches Institut und Museum der Eidgenössischen Technischen Hochschule. This collection includes much of the material, described by Oswald Heer, from Oeningen.

IV. SYSTEMATIC PALAEONTOLOGY: SYNONYMIC LIST OF FOSSIL BEES (EXCLUDING APIDAE)

The following list is arranged according to Michener (1944, 1965). His phylogenetic groups and main diagnostic characters for families, relevant subfamilies and tribes have been quoted, even though it is sometimes doubtful whether they are applicable to fossil forms. Indeed, only completely inapplicable characters have been omitted.

In compiling the list a considerable number of specimens have been examined. In the case of unexamined material, no diagnoses of genera or species or systematic descriptions are given. These must await a study of the fossil material in American collections. Among such material, too, those specimens whose affinities have been stated in a definite way by earlier authors, but concerning which one might hold other views, have sometimes been accorded the benefit of the doubt, and noted under the generic name assigned by the most trustworthy author. The sections headed '*incertae sedis*' therefore do not include specimens which are believed to be of such a nature that more information about them may substantiate their present suggested status. It is reserved for those which are too poorly preserved to be classifiable, and for vague records which cannot be substantiated by specimens.

The publication containing the first valid name in accordance with the International Rules of Zoological Nomenclature has been marked with an asterisk (*).

Superfamily **APOIDEA** Ashmead 1899

Family **COLLETIDAE** Bingham 1897

DIAGNOSIS. Labrum broader than long; subantennal areas absent or at least reduced to small triangular spaces; lower sides of clypeus not bent parallel to long axis of body ; subantennal sutures directed toward inner margins of antennal sockets ; facial foveae often present ; galeae short post-palpally and usually short pre-palpally, glossa short and often truncate or bifid, rarely round ; labial palpi short, segments similar but sometimes the first somewhat elongated and broadened ; pre-episternal sutures usually complete ; metanotum usually horizontal ; middle coxae, as seen from the outside, much shorter than the distance from their summits to posterior wing bases ; pygidial plate present or absent.

Many of the genera are also distinguished from practically all other bees in having the posterior part of vein 2nd m-cu (2nd recurrent) of each forewing arcuate towards the apex of the wing ; the basal vein is not strongly curved.

REMARKS. No fossil Colletidae have so far been found,[2] though *Cyrtapis*, a genus of Halictidae, is according to Cockerell (1908a) in some respects reminiscent of the Colletidae.

Family **HALICTIDAE** Ashmead 1899

DIAGNOSIS. Labrum broader than long, but in some females its apex is produced to form a broad, acutely pointed process ; subantennal areas absent, though there is usually a single subantennal suture directed towards inner margins of antennal sockets ; lower sides of clypeus not bent back parallel to long axis of body ; facial foveae ordinarily absent ; galeae elongated pre-palpally, not post-palpally, the pre-palpal section tapering evenly to an acute base ; labial palpi with segments similar to each other, and usually cylindrical, rarely are any of the first three elongate and flattened. Glossa acute, usually short, without flabellum ; pre-episternal sutures usually complete ; metanotum horizontal ; middle coxae with exposed parts much shorter than distance from summits to posterior wing bases ; basitibial plate usually present in females, except in parasitic genera ; pygidial plate present in females.

Basal vein usually strongly curved ; jugal lobe of posterior wings much more than half as long as anal lobe.

The most distinctive features are the long pre-palpal parts of the galeae, the usually strong arcuation or angulation of the 1st abscissa of basal vein (vein M), and the normally complete pre-episternal suture.

DISTRIBUTION. Oligocene to Recent.

REMARKS. Apart from the genus *Cyrtapis*, which has colletid affinities, only true Halictinae are known as fossils. By Oligocene times they appear to have been very modern in wing venation and probably in their general appearance also.

Subfamily **HALICTINAE** Ashmead 1899

DIAGNOSIS. Supraclypeal area convex and protuberant if seen in profile ; clypeus itself longer than labrum and not protuberant much beyond level of supraclypeal area ; labrum in females commonly provided with a broad, pointed apical process ;

---

[2] But see Appendix, p. 255.

antennal sockets not, or only a little, below middle of face ; pre-episternal suture conspicuous and complete ; scopa, when present, usually very extensive and found on posterior trochanters, femora, tibiae and basitarsi ; prepygidial fimbria usually divided by a longitudinal line without hairs or with only appressed hairs.

First abscissa of basal vein (vein M) strongly arcuate and first submarginal cell ordinarily longer than third when, as is usually the case, three are present.

Sometimes the glossa is elongated and variously modified ; the labial palpi are not elongated.

Remarks. This large subfamily is only very moderately represented by fossils.

Genus ***CYRTAPIS*** Cockerell 1908

*1908a *Cyrtapis* Cockerell : 339.
1909b *Cyrtapis* Cockerell ; Cockerell : 80.

Genotype. *Cyrtapis anomalus* Cockerell by monotypy.

Remarks. According to Cockerell (1908a), 'the general appearance and the large stigma, marginal cell, and bent basal nervure are all as in the Halictines. The form of the second submarginal cell, with the first r.n. joining it before the middle, as well as the second r.n. with the double curve, suggest affinity with the Colletines'. *Cyrtapis* may well have retained primitive elements, but because its evolution is towards the Halictines it is better to look upon it, for the time being at least, as a representative of the latter. Special mention of the type was made by Cockerell (1909b).

Cyrtapis anomalus Cockerell 1908

*1908a *Cyrtapis anomalus* Cockerell : 339.
1909b *C. anomalus* Cockerell ; Cockerell : 80.
1931 *Cyrtapis anomalus* Cockerell ; Salt : 145.

Holotype. Cockerell Collection, whereabouts unknown.

Distribution. Oligocene : Florissant.

Remarks. Mouth parts not known. In the circumstances, and because vein 2nd m-cu (2nd recurrent) has a strong double bend, the species is considered to be a little anomalous.

Genus ***HALICTUS*** Latreille 1804

*1804 *Halictus* Latreille : 182.
1935b *Halictus* Latreille ; Richards : 170.
1938 *Prohalictus* Armbruster : 48, fig. 74 (type species : *P. schemppi* Armb.).

Genotype. *Apis quadricincta* Fabricius, by subsequent designation of Richards (1935b : 170).

Halictus ruissatelensis Timon-David 1944

1943 *Sphecodes* Timon-David : 256.
*1944 *Halictus ruissatelensis* Timon-David : 42.

HOLOTYPE. Timon-David Collection, Marseille.

DISTRIBUTION. Oligocene : Bassin de Marseille.

REMARKS. Originally included by Timon-David (1943) in *Sphecodes*, but later (1944) placed, more correctly, in *Halictus*. We have not examined the specimen.

Halictus florissantellus Cockerell 1906

*1906 *Halictus florissantellus* Cockerell : 43.
1907 *Halictus florisantellus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2010 (= Scudder Coll. No. 921).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. The name '*florisantellus*' (Handlirsch 1907) is obviously a printer's error. Cockerell (1906) writes that only part of the wing venation is preserved, but 'generic reference seems safe'. Approximately 6·5 mm long.

Halictus miocenicus Cockerell 1909

*1909a *Halictus miocenicus* Cockerell : 160.
1931 *Halictus miocenicus* Cockerell ; Salt : 146.

HOLOTYPE. Cockerell Collection, whereabouts unknown.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell, the generic position is probably correct.

Halictus scudderiellus Cockerell 1906

*1906 *Halictus scudderiellus* Cockerell : 43.
1907 *Halictus Scudderiellus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2011 (= Scudder Coll. No. 1966).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Appears to be correctly placed. This bee is smaller than *H. florissantellus*, being only 4·5 mm long.

Halictus schemppi (Armbruster 1938)

*1938 *Prohalictus schemppi* Armbruster : 48, fig. 74.

HOLOTYPE. Schempp Collection, Stuttgart-Weil.

PARATYPES. Three specimens, Armbruster Collection.

DISTRIBUTION. Miocene : Randeck.

Remarks. Armbruster refers to one of his specimens as a true *Halictus*, stating (1938 : 48) that 'the nervulus is positioned quite normally'. There is no reason for believing the others are not conspecific.

Family **ANDRENIDAE** Latreille 1802

Diagnosis. Labrum broader than long, subantennal areas defined by two subantennal sutures beneath each antennal socket ; anterior lateral margins of clypeus usually concave ; lower sides of clypeus bent backwards more or less parallel to long axis of body (except in many species of *Andrena*) but clypeus not strongly protuberant ; facial foveae usually present ; galeae short pre-palpally and usually so post-palpally ; labial palpi short, the segments similar or first segment elongated and flattened, very rarely first two segments elongated ; glossa short or long, acute, without a flabellum ; pre-episternal sutures absent or present below scrobal sutures ; metanotum horizontal ; middle coxae short as seen externally, far shorter than distance from summits to posterior wing bases. Basitibial and pygidial plates present in females.

Jugal lobe of posterior wing at least nearly three-quarters as long as anal lobe.

The most characteristic feature of this family is the presence of defined subantennal areas. Unfortunately, in some species they lie below the bases of the antennae, covered with hairs, and even when uncovered only weak sutures may be revealed.

Distribution. Eocene to Recent.

Remarks. Only the subfamilies Andreninae and Panurginae are represented among the fossils. *Andrena* was well characterized as a genus by the Eocene.

Subfamily **ANDRENINAE** Latreille 1802

Diagnosis. Facial foveae large and usually covered with minute hairs giving a golden or reddish brown sheen in females, but in males foveae absent or virtually undefined and not clothed with minute hairs ; first flagellar segment rarely a little more than half as long as scape, usually much shorter ; maxillary palpi six-segmented ; segments of labial palpi cylindrical, similar to one another ; glossa usually short, acute ; pre-episternal sutures absent below scrobal sutures ; scopa present from coxae to basitarsi of posterior legs.

Pterostigma moderate to large in size ; marginal cell longer than distance from apex to wing tip, and with the apex itself pointed on the costal margin of the wing or very narrowly rounded.

Remarks. Most fossil members of this subfamily belong to the important genus *Andrena*, and two have been placed in the extinct genera *Lithandrena* and *Pelandrena*.

Genus ***ANDRENA*** Fabricius 1775

*1775 *Andrena* Fabricius : 376.
1873 *Biareolina* Dours : 288 (type species : *B. neglecta* Dours).
1912 *Andrena* Fabricius ; Viereck : 613.

GENOTYPE. *Apis helvola* Linnaeus 1758, by subsequent designation of Viereck (1912 : 613).

DISTRIBUTION. Eocene to Recent.

Andrena wrisleyi Salt 1931

*1931 *Andrena wrisleyi* Salt : 141, fig. 1.

HOLOTYPE. Formerly in the Geol. Museum, Univ. Koenigsberg, but now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Well figured and described.

Andrena clavula Cockerell 1906

*1906 *Andrena* (?) *clavula* Cockerell : 45.
1907 *Andrena* (?) *clavula* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2014 (= Scudder Coll. No. 6963).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Considered by Cockerell (1906) to be congeneric with *A. sepulta*. He remarked, however, that 'the shape of the abdomen is like that of a ♀ *Ceratina*, or possibly certain Halictines, but the venation does not agree with these'.

Andrena grandipes Cockerell 1911

*1911a *Andrena grandipes* Cockerell : 73.
1931 *Andrena grandipes* Cockerell ; Salt : 145.
1938 *Andrena grandipes* Cockerell ; Rodeck : 295.

HOLOTYPE. Univ. Colorado Mus., No. 8599 (with counterpart).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1911a) states 'agrees closely with modern *Andrena* in most respects, but is peculiar for the very broad hind tibia and basitarsus, the small eyes and the long slender marginal cell'.

Andrena hypolitha Cockerell 1908

*1908b *Andrena hypolitha* Cockerell : 328.
1931 *Andrena hypolitha* Cockerell ; Salt : 145.
1938 *Andrena hypolitha* Cockerell ; Rodeck : 295.

HOLOTYPE. Univ. Colorado Mus., No. 18736.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Differs from *A. sepulta* and *A. clavula* in various details of venation etc. It is not clear, however, how the abdomen differs from *A. clavula*.

Andrena lagopus Latreille 1809

*1809 *Andrena lagopus* Latreille : 151.
1873 *Biareolina neglecta* Dours : 288.
1913a *Biareolina neglecta* Dours ; Cockerell : 346.
1930 *Andrena lagopus* Latreille ; Schmiedeknecht : 942.

HOLOTYPE. Recent, whereabouts unknown.

FOSSIL SPECIMEN. Possibly in the United States National Museum.

DISTRIBUTION. Oligocene : probably Florissant. Also Recent.

REMARKS. Schmiedeknecht, in identifying his specimen with a Recent species, mentions but one character, namely that the side of the stigma on the marginal cell 'is conspicuously angulate or subdentate about the middle'.

Biareolina Dours is a synonym of *Andrena* Fabricius, but since it possesses two submarginal cells, it is sometimes accorded separate generic status, a practice not followed by Michener (1944). Moreover, the reduction of the number of submarginal cells from three to two occurs frequently within the same species, for instance in *Andrena, Halictus, Nomada* and others.

Andrena percontusa Cockerell 1914

*1914 *Andrena percontusa* Cockerell : 640.
1931 *Andrena percontusa* Cockerell ; Salt : 145.

HOLOTYPE. Wickham Collection, ? Peabody Museum, Yale.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Venation like *A. sepulta* and *A. clavula*, but a small species. Abdomen differs in shape from *A. clavula*. According to Cockerell (1914), the species can be distinguished from *A. grandipes* and *A. hypolitha* by the venation.

Andrena sepulta Cockerell 1906

*1906 *Andrena sepulta* Cockerell : 44.
1907 *Andrena sepulta* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2013 (= Scudder Coll. No. 14288).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1906) states 'the venation is not exactly like that of any modern species with which I have compared it but the differences are unimportant'.

Andrena primaeva Cockerell 1909

(Pl. 1, fig. 2)

1865 Drei Osmien ; Heer : 386 (*partim*).
1876 Osmiae ; Heer : 43 (*partim*).
1909c Three species of *Osmia* ; Cockerell : 316 (*partim*).
*1909c *Andrena* (?) *primaeva* Cockerell : 316.
1909c *Osmia primaeva* (Heer MS) ; Cockerell : 316.
1931 *Andrena* (?) *primaeva* Cockerell ; Salt : 145.

Holotype. Eidgenössische Technische Hochschule, Zürich, No. SN.202, with counterpart.

Distribution. Miocene : Oeningen.

Description and Remarks. Although Cockerell's references to Osmiae are, on the whole, difficult to interpret, there is no doubt whatever that the specimen he described as *Osmia primaeva* was the holotype. The insect is reasonably well preserved but the head is lacking. The chitin is dark brown in colour which may have been the colour of the original insect. The abdomen is plump and subglobose, but, since it is a millimetre broader than the thorax, the junction of the two gives the impression of a distinct constriction.

The thorax has a large convex mesoscutum and apparently strong tegulae ; the other features are indistinct.

The hind legs are fairly well preserved, the tibia and basitarsus being approximately equal, their combined length being 3·5 mm ; the tibia is broad, apparently twice the width of the basitarsus, and both are copiously hairy ; the femur is as broad as the tibia. The tibia and basitarsus of the middle leg are not preserved in a natural position, and we are inclined to consider Cockerell's basitarsus as the tibia and his tibia as the femur. Both femur and tibia are of the same width, but the tibia is slightly longer.

The wings are not preserved in their entirety owing to a crack in the rock. Fortunately, what is preserved is very distinct and includes the apical region of the fore and hind wings.

Forewing : long, well-developed pterostigma ; marginal cell narrowing apically, and arising broadly from the pterostigma ; three submarginal cells, the first not completely preserved, the second rhomboid, receiving the first recurrent vein slightly distad of the middle and having its proximal cross vein slightly hooked at the base, the third submarginal cell at least twice as large as the second, only half as broad on the marginal cell as its own base, and receiving the second recurrent vein in its last third.

Hindwing : radial sector and media continued to wing margin and cross-vein r-m only very slightly oblique.

Cockerell's (1909) statement that 'all things considered the reference to *Andrena* seems reasonably assured' appears a fair conclusion. The venation of the hind wing and the rather plump body precludes the specimen from being referred to *Halictus*.

Measurements. Length of thorax and abdomen (head lacking) 7 mm ; length of thorax 2·25 mm, width 3 mm ; length of abdomen 4·75 mm, width 4 mm.

Andrena sp. indet. (Brischke)

1886 *Andrena* Brischke : 278.
1891 *Andrena* Brischke ; Scudder : 686 (5915).
1907 *Andrena* Brischke ; Handlirsch : 890.
1931 *Andrena* sp. Brischke ; Salt : 144.

Distribution. Eocene : Baltic amber.

REMARKS. Among Menge's and Helm's collections, investigated by Brischke, were apparently two specimens generically determined as *Andrena*, but not described.

Andrena sp. indet. (Motschulsky)

1856 *Andrena* Motschulsky : 28.
1931 *Andrena* sp. Motschulsky ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Motschulsky merely records the occurrence of the genus.

Genus ***LITHANDRENA*** Cockerell 1906

*1906 *Lithandrena* Cockerell : 44.
1909b *Lithandrena* Cockerell ; Cockerell : 81.

GENOTYPE. *Lithandrena saxorum* Cockerell 1906 by monotypy.

REMARKS. According to Cockerell, 'a genus of Andrenidae, allied to *Andrena*. It differs from *Andrena* and *Nomia* in the second r.n. which is strongly bent in its upper part, straight but oblique below ; from *Andrena* alone it differs in the proportions of the submarginal cells ; and from *Nomia* also by the tip of the marginal cell, which is pointed, and a little away from the costae. The general appearance is that of an *Andrena*, but it cannot be referred to this or any other genus . . .'. Special mention of the type was made by Cockerell (1909b).

Lithandrena saxorum Cockerell 1906

*1906 *Lithandrena saxorum* Cockerell : 44.
1907 *Lithandrena saxorum* Cockerell ; Handlirsch : 889.
1909b *Lithandrena antiquorum* Cockerell ; Cockerell : 80.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2012 (= Scudder Coll. No. 8219).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Length 8·6 mm. Venation of forewing fully described (Cockerell 1906). Head as wide as thorax, black ; flagellum stout ; abdomen light in colour with a broad entire dark band on each segment, legs hairy.

Genus ***PELANDRENA*** Cockerell 1909

*1909a *Pelandrena* Cockerell : 159.
1909b *Pelandrena* Cockerell ; Cockerell : 81.

GENOTYPE. *Pelandrena reducta* Cockerell 1909a by monotypy.

REMARKS. Allied to *Andrena* but with two submarginal cells on the anterior wing. Special mention of the type was made by Cockerell (1909b). The reason for the erection of this genus is not clear. It may be based only on the two submarginal cells, in which case its generic status is weak.

Pelandrena reducta Cockerell 1909

*1909a *Pelandrena reducta* Cockerell : 160.
1909b *Pelandrena reducta* Cockerell ; Cockerell : 81.
1931 *Pelandrena reducta* Cockerell ; Salt : 146.
1938 *Pelandrena reducta* Cockerell ; Rodeck : 298.

HOLOTYPE. Univ. Colorado Mus., No. 18741.

DISTRIBUTION. Oligocene : Florissant.

Subfamily **PANURGINAE** Leach 1815

DIAGNOSIS. Facial foveae, when present, much smaller than in Andreninae, not clothed with fine hairs, and frequently distinct in males as well as in females ; labial palpi frequently with first segment much elongated ; maxillary palpi usually six-segmented (reduced in some species of *Perdita*). Scopa primarily confined to posterior tibiae and basitarsi.

Pterostigma usually rather large ; marginal cell, which is normally not longer than distance from its own apex to apex of wing, mostly obliquely truncate apically but sometimes merely bent away from wing margin.

REMARKS. Only one fossil genus belongs to this subfamily.

Genus ***LIBELLULAPIS*** Cockerell 1906

*1906 *Libellulapis* Cockerell : 42.
1909b *Libellulapis* Cockerell ; Cockerell : 80.

GENOTYPE. *Libellulapis antiquorum* Cockerell 1906 by monotypy.

REMARKS. Cockerell (1913a), when discussing *Libellulapis wilmattae,* stated, 'A reconsideration of the genus leads me to place it in the Panurgidae where, by reason of certain features of the venation, it appears to stand rather near to *Panurgus*'. Eyes curiously prominent. Special mention of the type was made by Cockerell (1909b).

Libellulapis antiquorum Cockerell 1906

*1906 *Libellulapis antiquorum* Cockerell : 42.
1907 *Libellulapis antiquorum* Cockerell ; Handlirsch : 889.
1909a *Libellulapis antiquorum* Cockerell ; Cockerell : 80.
1938 *Libellulapis antiquorum* Cockerell ; Rodeck : 297.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2009 (= Scudder Coll. No. 9061).

PARATYPE. Univ. Colorado Mus., No. 18740 (= Scudder Coll. No. 8560).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1906) considered this species different from *Halictoides maurus* (Cresson), *Hesperapis rhodoceratus* (Cockerell) and *Parandrena andrenoides* Cresson in points of venation, and believed that it did not agree with *Diandrena* or *Biareolina*.

Libellulapis wilmattae Cockerell 1913

*1913a *Libellulapis wilmattae* Cockerell : 344, figs 2, 3.
1931 *Libellulapis wilmattae* Cockerell ; Salt : 146.
1938 *Libellulapis wilmattae* Cockerell ; Rodeck : 297.

HOLOTYPE. U.S. Nat. Mus., No. 58688. Counterpart, Univ. Colorado Mus., No. 18742.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1913a) states, 'Broad head and prominent eyes as in some Panurgi, pygidial plate as in *Dasypoda*'.

Family **ANDRENIDAE** *incertae sedis*

Andrenidae gen. et sp. indet. (Handlirsch)

1907 (? Andrenidae) ; Handlirsch : 890.
1931 Andrenidae ? sp. (Handlirsch) ; Salt : 144.

MATERIAL. Hofmuseum, Vienna.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Hind leg with pollen. Head formation suggestive of *Halictus* or *Andrena*.

Andrenidae gen. et sp. indet. (Scudder)

1881 Andrenidae ; Scudder : 290.
1883 Andrenidae ; Scudder : 280.
1891 (Andrenidae) (several) ; Scudder : 682 (5872).
1907 (Andrenidae) (mehrere) Scudder ; Handlirsch : 890.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Specimens appear to be poorly preserved.

Family **MELITTIDAE** Dumeril 1821

DIAGNOSIS. Labrum broader than long ; subantennal areas absent ; subantennal sutures directed, except sometimes at their upper ends, towards inner margins of antennal sockets ; lower sides of clypeus not, or only a little, bent backwards ; clypeus not protuberant. Facial foveae absent ; galeae short pre-palpally and usually so post-palpally ; labial palpi with segments similar to one another, cylindrical ; glossa short or long, acute ; pre-episternal and scrobal sutures usually absent, the former always absent below the latter ; metanotum horizontal or subhorizontal ; middle coxae short as seen externally, much shorter than distance from their summits to posterior wing bases ; scopa confined to posterior tibiae and basitarsi, although trochanters and femora are hairy ; basitibial plates and pygidial plate present in female.

DISTRIBUTION. Eocene to Recent.

Remarks. The subfamilies Ctenoplectrinae and Melittinae only are represented among the fossils.

Subfamily **CTENOPLECTRINAE** Cockerell 1920

Diagnosis. Scrobal and upper parts of pre-episternal sutures are present, though of doubtful value for fossil forms ; inner hind tibial spur much broadened basally and throughout its length provided with a comb of very many long fine teeth ; posterior basitarsi of female nearly as broad as tibiae ; pygidial plate of male absent, that of female narrow apically, greatly broadened basally.

Pterostigma hardly twice as long as broad ; marginal cell considerably longer than distance from its apex to wing tip and bent gradually away from wing margin for nearly half length of cell ; two submarginal cells ; jugal lobe of posterior wing about half as long as anal lobe.

Remarks. Among Recent forms this subfamily contains only the genus *Ctenoplectra* found from Australia and Africa to China. This genus, however, is not yet known in the fossil state. On the other hand, the subfamily is represented by two fossil genera *Ctenoplectrella* and *Glyptapis*. Moreover, Cockerell (1909d) maintained that the genera included in this subfamily are 'so remote from the modern members of that group that they at least form a distinct subfamily, Glyptapinae'. 'That group', however, refers to the Megachilidae to which *Ctenoplectra*, and hence *Ctenoplectrella* etc., was considered to belong. Therefore until the affinities of the *Ctenoplectra* group, both fossil and Recent, have been more clearly defined, it is not considered advisable to create a new subfamily.

Genus ***CTENOPLECTRELLA*** Cockerell 1909

*1909c *Ctenoplectrella* Cockerell : 314.
1909d *Ctenoplectrella* Cockerell ; Cockerell : 19.

Genotype. *Ctenoplectrella viridiceps* Cockerell 1909 by monotypy.

Remarks. This genus appears to be closely related to *Glyptapis*. Both genera have *Ctenoplectra* as 'their nearest relative in the modern fauna'. *C. viridiceps* was first mentioned by Cockerell (1909c) with some characters, but its full description followed in a later paper (1909d). [See also Appendix, p. 255.]

Ctenoplectrella dentata Salt 1931

*1931 *Ctenoplectrella dentata* Salt : 139.

Holotype. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

Distribution. Eocene : Baltic amber.

Remarks. Salt considers it possible that this specimen is the male of *Ctenoplectrella viridiceps* Cockerell and gives a good description and figures.

Ctenoplectrella viridiceps Cockerell 1909

*1909c *Ctenoplectrella viridiceps* Cockerell : 314.
1909d *Ctenoplectrella viridiceps* Cockerell ; Cockerell : 19, fig. 14.
1931 *Ctenoplectrella viridiceps* Cockerell ; Salt : 145.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Female, see above. This species was a small, black, stout bee, like *Glyptapis*, hardly 5 mm long. 'The eyes were bare and the sting visible'. Full description given by Cockerell (1909d).

Genus ***GLYPTAPIS*** Cockerell 1909

*1909c *Glyptapis* Cockerell : 314.
1909d *Glyptapis* Cockerell ; Cockerell : 13.

GENOTYPE. *Glyptapis mirabilis* Cockerell, by original designation.

REMARKS. This genus, together with *Ctenoplectrella*, is referred by Cockerell 'to a group from which the Megachiloids sprang'. The genus was mentioned (1909c) in connection with *G. mirabilis*, but it was not described until later (1909d).

Glyptapis fuscula Cockerell 1909

*1909d *Glyptapis fuscula* Cockerell : 17, fig. 12.
1931 *Glyptapis fuscula* Cockerell ; Salt : 145.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Cockerell (1909d) mentions that the ventral side of the abdomen is clearly seen to be furnished with strong bristles, the beginning of a ventral scopa. As distinctive characters of the species he gives the very dark wings and the large stigma.

Glyptapis mirabilis Cockerell 1909

*1909c *Glyptapis mirabilis* Cockerell : 314.
1909d *Glyptapis mirabilis* Cockerell ; Cockerell : 14, figs 9, 10.
1931 *Glyptapis mirabilis* Cockerell ; Salt : 146.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. The genotype, selected by Cockerell (1909d), is actually the monotype, since the genus and species were first mentioned (1909c) together, with a few descriptive words. The specific characters are the dark brown stigma and veins, the length of the marginal cell (over 1·2 mm), the entirely black body and the punctate mesothorax.

Glyptapis neglecta Salt 1931

*1931 *Glyptapis neglecta* Salt : 136, fig. 1.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Well described and figured by Salt. This is the largest known *Glyptapis* from the Baltic amber.

Glyptapis reducta Cockerell 1909

*1909d *Glyptapis reducta* Cockerell : 18, fig. 13.
1931 *Glyptapis reducta* Cockerell ; Salt : 146.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Wings hyaline. Cockerell (1909d) regards the ferruginous stigma and veins and the length of the marginal cell (0·935 mm) as diagnostic.

Glyptapis reticulata Cockerell 1909

*1909d *Glyptapis reticulata* Cockerell : 16, fig. 11.
1931 *Glyptapis reticulata* Cockerell ; Salt : 146.
1969 *Glyptapis reticula* Cockerell ; Kellner-Pillault : 521.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Differs from *G. mirabilis* chiefly in the metallic crimson tints on the abdomen and the reticulate mesothorax.

Subfamily **MELITTINAE** Dumeril 1821

DIAGNOSIS. Inner hind tibial spur unmodified ; posterior basitarsi more slender than tibiae (except in male *Haplomelitta*) and shorter than tibiae ; distitarsi unusually large.

Pterostigma slender, more than twice as long as broad, its margins basad of vein are very rarely converging basally ; marginal cell longer than distance from its own apex to wing tip, the apex itself very narrowly rounded on wing margin and bent away from the latter, if at all, only apically ; three submarginal cells, second much the smallest, the first being the largest ; jugal lobe of posterior wing nearly half as long as anal lobe (rarely three-quarters).

The species of this subfamily are of moderate size, and black. The abdomen is provided with pale pubescent fasciae, giving the appearance of certain species of *Halictus* and *Andrena*.

REMARKS. This subfamily is represented, among fossils, only by the genus *Melitta*.

Genus ***MELITTA*** Kirby 1802

*1802 *Melitta* Kirby : 130–134.
1935b *Melitta* Kirby ; Richards : 172.

GENOTYPE. *Melitta tricincta* Kirby 1802, selected by Richards (1935 : 172).

Melitta willardi Cockerell 1909

*1909e *Melitta willardi* Cockerell : 393.
1931 *Melitta willardi* Cockerell ; Salt : 146.
1938 *Melitta willardi* Cockerell ; Rodeck : 297.

HOLOTYPE. Univ. Colorado Mus., No. 18737.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1909e) writes, 'Venation normal for *Melitta*, except that the upper segment of the basal nervure is shorter' ; also 'the reference of this insect to *Melitta* seems safe'.

Family **MELITTIDAE** ***incertae sedis***

Dasypoda (s.l.) sp. indet. (Menge)

1856 *Dasypoda* Menge : 26.
1891 *Dasypoda* (vic.) Menge ; Scudder : 696 (6005).
1907 *Dasypoda* (vic.) Menge ; Handlirsch : 890.
1931 *Dasypoda* vic. Menge ; Salt : 144.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. An 'Andrenida, Grabwespen' was reported (Menge 1856) to resemble *Dasypoda* but 'was distinguished from it by the hind basitarsus having a blunt lateral process in front of the joint with the second tarsal segment, and the hind leg being longer than the abdomen' (transl.). The mandibles had a broad tip with three teeth and the lancet-shaped tongue had labial palps protruding. Two specimens existed, one clearly visible, the other covered with 'schimmel'.

Family **MEGACHILIDAE** Latreille 1802

DIAGNOSIS. Labrum longer than broad, widened basally to form a long line of articulation with clypeus ; subantennal areas absent ; subantennal sutures directed towards outer margins of antennal sockets ; lower sides of clypeus not bent backwards parallel to long axis of body ; facial foveae absent ; first flagellar segment much shorter than scape ; galeae short pre-palpally, long post-palpally ; labial palpi with first two segments elongated and flattened, sheath-like, first segment usually shorter than second ; glossa linear, possessing a flabellum, pre-episternal and scrobal sutures considerably reduced or absent ; metanotum usually vertical, sometimes horizontal ; middle coxae elongate, at least half, and usually more than half, as long as distance from summits to hindwing bases ; basitibial plates absent ; scopa, when present, confined to abdominal sterna ; pygidial plate absent, except in *Lithurge*.

Pterostigma small ; submarginal cells two, the second as long, or nearly as long, as the first ; marginal cell pointed or narrowly rounded at apex, which is usually a little bent away from costal margin of wing and nearer to wing tip than to base of cell.

The most distinguishing characters are the position of the scopa, the form of the labrum and the direction taken by the subantennal sutures.

DISTRIBUTION. Eocene to Recent.

REMARKS. The subfamilies Lithurginae and Megachilinae are known as fossils, the latter being well represented in the Oligocene.

Subfamily **LITHURGINAE** Newman 1834

DIAGNOSIS. Face of female elevated below antennal sockets ; epistomal suture in most part absent ; mandibles in both sexes short and robust, tridentate, the middle tooth longer and more elevated than the others ; metanotum about one-eighth as long as scutellum ; coarse spiculae of tibiae arranged in two longitudinal rows on fore and middle legs, scattered on posterior legs ; posterior basitarsi slender, parallel-sided, about as long as posterior tibiae ; second abdominal tergum unusually small, posterior margin broadly rounded ; terga two to seven of male exposed and unmodified ; male with pygidial plate, female with slender remnant thereof in the form of large spine, flattened dorsally.

Jugal lobe of posterior wing about three-quarters as long as anal lobe.

REMARKS. Only one genus, *Lithurge*, is known to which both Recent and fossil forms belong.

Genus ***LITHURGE*** Latreille 1825

*1825 *Lithurge* Latreille : 463.
1827 *Lithurgus* Berthold : 467.

GENOTYPE. *Centris cornuta* Fabricius 1787 by monotypy.

Lithurge adamitica (Heer 1865)

*1865 *Apis adamitica* Heer : 386, fig. 287.
1867 *Apis adamitica* Heer ; Heer : 4, pl. 3, fig. 11.

1872 *Apis adamitica* Heer ; Heer : 473, fig. 287.
1876 *Apis adamitica* Heer ; Heer : 43, fig. 287.
1879 *Apis adamitica* Heer ; Heer : 412, fig. 329.
1891 *Apis adamitica* Heer ; Scudder : 688 (5936).
1907 *Apis adamitica* Heer ; Handlirsch : 892.
1909c *Lithurgus adamiticus* (Heer) ; Cockerell : 313.
1915 *Apis adamitica* Heer ; v. Buttel-Reepen : 9, fig. 1.
1928 *Apis adamitica* Heer ; Wheeler : 97.
1928 *Lithurgus* Berthold ; Wheeler : 97.
1931 *Apis adamitica* Heer ; Statz : 45.
1938 '*Apis adamitica*' (Heer) ; Armbruster : 86.

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, V.S.4.

OTHER SPECIMENS. (1) Eidgenössische Technische Hochschule, Zürich, SN.200 ; (2) Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1216 (Oe.95).

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. Cockerell (1909c) considered this species to be somewhat more primitive than recent *Lithurge*, possibly a near subgenus. According to him it is separated from *Apis* by its possession of only two submarginal cells. Unfortunately the holotype, which we have studied, is not well preserved and we have not succeeded in recognizing the submarginal cells. Armbruster (1938) who contributed some original remarks on it did not consider it to belong to *Apis*.

The holotype, indeed, is a somewhat elongated insect with a slender and pointed abdomen. The outlines of the wings are preserved but the venation is mostly too indistinct for satisfactory recognition. It is clear, however, that the species does not belong to the genus *Apis*, and also that the preservation of the specimen appears to have deteriorated since it was examined by Cockerell.

The following points are presented as still being of interest. The head and thorax have preserved no recognizable diagnostic characters ; the colour of the body has darkened from Cockerell's 'warm, red-brown' ; the abdomen, as Cockerell stated, is 'truncate basally, pointed apically' and, since basal intersegmental membranes are evident, may be somewhat distended ; legs are lacking ; wings are small in comparison with size of insect, and wing venation shows only the following points. Strong costal vein ; straight and short basal vein, the anterior section of which is longest ; short, stubby, pointed marginal cell ; poorly developed pterostigma. The apex of the wing, marginal cells and recurrent nerves are no longer clearly evident ; the cross vein cu-a, however, can be detected slightly distal of the juncture of basal vein on cu. While these characters obviously do not give sufficient grounds for placing the specimen generically, we must recognize that Cockerell saw it while in a better state of preservation and accept his decision in this matter.

A second specimen (Zürich, SN.200) has been studied and tentatively assigned to this species. Its head, thorax and abdomen (except the tip) are quite well preserved, but the wings are present only in traces and the legs are missing. A strong costal vein is present, and a marginal cell similar to *Lithurge*.

A third specimen (Karlsruhe, Inv.1216 (Oe.95)) may also belong here. Abdomen and thorax alone are preserved. The former, however, is well segmented and pointed, and is very reminiscent of the holotype, from which it differs only slightly in size, i.e. length of abdomen 10 mm, as compared with 8·5 mm for the holotype. The width of the abdomen is 4·25 mm and the overall length, as preserved, i.e. without head, is 13 mm.

Finally, it is interesting to note that Heer's figure (1865 : fig. 287) differs in wing venation from his pl. 3, fig. 11 (1867), although both are presumably meant to represent the same specimen.

Subfamily **MEGACHILINAE** Latreille 1802

Diagnosis. Face of female very rarely elevated below antennal sockets ; epistomal suture complete ; mandibles variously toothed, apical tooth longest, preapical tooth not elevated ; tibiae not spiculate ; posterior basitarsi much shorter than tibiae ; second abdominal tergum large, with the posterior margin usually straight, so that base of abdomen lacks the compressed aspect of *Lithurge* ; abdomen of male with fewer unmodified sterna than in *Lithurge* ; pygidial area entirely absent.

Jugal lobe of posterior wings less than half as long as anal lobe.

Remarks. Two tribes, Anthidiini and Megachilini, are distinguished within this subfamily, both known as fossils.

Tribe **ANTHIDIINI** Michener 1944

Diagnosis. Posterior margin of scutellum usually vertical or even overhanging, at a distinct angle to the dorsal surface ; integumental maculation, at least in part, pale ; claws of female cleft or at least with an inner tooth.

Inner margin of pterostigma from its base to the base of medial vein little, if at all, longer than width of pterostigma.

Remarks. Two Recent genera are represented by fossils, and there is one extinct genus. [See also Appendix, p. 256.]

Genus ***ANTHIDIUM*** Fabricius 1805

*1805 *Anthidium* Fabricius : 364.
1810 *Anthidium* Fabricius ; Latreille : 439.

Genotype. *Apis manicata* Linnaeus 1758, selected by Latreille (1810 : 439).

Anthidium mortuum (Meunier 1920)

*1920 *Eucera mortua* Meunier : 731, pl. 1, fig. 5, text-fig. 4.
1931 *Eucera mortua* Meunier ; Salt : 145.
1936 *Anthidium mortuum* (Meunier) ; Statz : 260, 285, 293, 294, pl. 13, fig. 38.

Holotype. Heimatmuseum Siegberg (Lahn), Bauckhorn Collection.

Distribution. Oligocene : Rott am Siebengebirge.

Remarks. This specimen was first described as *Eucera* by Meunier (1920). Statz (1936), on re-examining the specimen, placed it in *Anthidium*. He insisted that the venation of the fossil form was identical with that of *Anthidium*, except for the 'nervulus' which is 'interstitial' in the fossil and 'postfurcal' in the Recent species. Since Statz was the more reliable worker of the two, we are placing this form in *Anthidium*. The possibility of a *Eucera* occurring in Rott should not, however, be wholly disregarded, since Statz is anxious to reinforce his identification by the ecological argument that *Anthidium* builds its nest in stalks and twigs, which agrees better with the Rott biotope than the steppe habitat of *Eucera*. Statz' (1936 : 260), however, states that Recent species of *Eucera* have the second recurrent vein meeting the second submarginal cell, whereas in Meunier's *Eucera mortua* it ends distad to the second submarginal cross vein as in the genus *Anthidium*.

It is also necessary to point out that Statz' discussion of this form is misleading. He describes it (1936 : 285) under the heading of 'new discoveries', whilst his figure proves it to be Meunier's holotype. Three further disconnected paragraphs appear (1936 : 260, 293, 294) in which no mention is made of the fact that he had no new specimen. The identity with Meunier's holotype is proved not only by the general shape of the fossil, but also by the frayed margin of the right forewing.

Anthidium exhumatum Cockerell 1906

*1906 *Anthidium exhumatum* Cockerell : 38.
1907 *Anthidium exhumatum* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2003 (= Scudder Coll. No. 13709, with counterpart, No. 11388).

PARATYPE. Scudder Coll. No. 8444.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell, 'not so typical an *Anthidium* as *A. scudderi*'. The paratype agrees with the holotype in the width of the marginal cell and the shape of the second discoidal. It differs in the strongly banded abdomen. He concludes, 'It appears to be a female and I have little doubt that it represents that sex in *A. exhumatum*'.

Anthidium scudderi Cockerell 1906

*1906 *Anthidium scudderi* Cockerell : 38.
1907 *Anthidium scudderi* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2002 (= Scudder Coll. No. 11381).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Apparently a typical *Anthidium* which can be clearly separated from *Megachile* on points of wing venation.

Genus ***DIANTHIDIUM*** Cockerell 1900

*1900 *Dianthidium* Cockerell : 412.

GENOTYPE. *Anthidium curvatum* Cockerell (*nec* Smith) – *Dianthidium sayi* Cockerell, by original designation (1900).

Dianthidium tertiarium Cockerell 1906

*1906 *Dianthidium tertiarium* Cockerell : 39.
1907 *Dianthidium tertiarium* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2004 (= Scudder Coll. No. 806).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. This average-sized (8 mm) dark brown bee can be assumed to be correctly placed by Cockerell, in view of his intimate knowledge of the genus.

Genus ***LITHANTHIDIUM*** Cockerell 1911

*1911b *Lithanthidium* Cockerell : 225.

GENOTYPE. *Lithanthidium pertriste* Cockerell 1911 by monotypy.

Lithanthidium pertriste Cockerell 1911

*1911b *Lithanthidium pertriste* Cockerell : 225.
1931 *Lithanthidium pertriste* Cockerell ; Salt : 146.
1938 *Lithanthidium pertriste* Cockerell ; Rodeck : 297.

HOLOTYPE. Univ. Colorado Mus., No. 18738.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Only a single specimen known.

Tribe **MEGACHILINI** Latreille 1802

DIAGNOSIS. Claws of female simple ; no obtrusive pale integumental maculation ; abdominal pattern often present, resulting from bands of pale hairs ; posterior part of scutellum, except in some parasitic forms, not separated by a sharp angle from dorsal surface.

Inner margin of pterostigma from its own base to base of radial vein much longer than width of pterostigma.

REMARKS. The Recent genera *Heriades, Megachile* and *Osmia* are represented by fossils.

Genus ***HERIADES*** Spinola 1808

*1808 *Heriades* Spinola : 7.
1810 *Heriades* Spinola ; Latreille : 439.

GENOTYPE. *Apis truncorum* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. According to Spinola's usage, the name *Heriades* is feminine. The masculine ending, however, is used here in conformity with modern usage.

Heriades bowditchi Cockerell 1906

*1906 *Heriades bowditchi* Cockerell : 41.
1907 *Heriades bowditchi* Cockerell ; Handlirsch : 889.
1938 *Heriades bowditchi* Cockerell ; Rodeck : 296.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2007 (= Scudder Coll. No. 13761).

PARATYPE. Univ. Colorado Mus., No. 18739 (= Scudder Coll. No. 13436).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Differs from *H. laminarum* in the pronouncedly larger head and the banded abdomen.

Heriades halictinus Cockerell 1906

*1906 *Heriades halictinus* Cockerell : 40.
1907 *Heriades halictinus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2006 (= Scudder Coll. No. 10564).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Resembles a small *Halictus* in superficial aspect, but its true affinity is indicated by wing venation. Differs from *H. laminarum* in its darker abdomen and smaller size.

Heriades laminarum Cockerell 1906

*1906 *Heriades laminarum* Cockerell : 40.
1907 *Heriades laminarum* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2005 (= Scudder Coll. No. 3062).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell maintains 'it appears to be allied to the ordinary species of *Heriades*'.

Heriades mersatus Cockerell 1923

*1923 *Heriades mersatus* Cockerell : 371.
1931 *Heriades mersatus* Cockerell ; Salt : 146.

HOLOTYPE. Supposedly in Colorado Museum of Natural History, but not referred to by Rodeck (1938).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Nearest to *H. halictinus*. Author 'sure' of genus.

Heriades mildredae Cockerell 1925

*1925a *Heriades mildredae* Cockerell : 420.
1931 *Heriades mildredae* Cockerell ; Salt : 146.
1938 *Heriades mildredae* Cockerell ; Rodeck : 296.

HOLOTYPE. Univ. of Colorado Mus., No. 15075, with counterpart.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell remarks that this species differs conspicuously from all other *Heriades.*

Heriades priscus Cockerell 1917

*1917 *Heriades priscus* Cockerell : 383.
1931 *Heriades priscus* Cockerell ; Salt : 146.

HOLOTYPE. U.S. Nat. Mus., No. 62543.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. The largest *Heriades* from Florissant. A robust, hairy, black insect. Cockerell did not appear to have much doubt about its generic position.

Heriades saxosus Cockerell 1913

*1913b *Heriades saxosus* Cockerell : 233.
1931 *Heriades saxosus* Cockerell ; Salt : 146.
1938 *Heriades saxosus* Cockerell ; Rodeck : 296.

HOLOTYPE. Univ. of Colorado Mus., No. 18638.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Nearest to *H. laminarum* Cockerell.

Genus ***MEGACHILE*** Latreille 1802

*1802a *Megachile* Latreille : 434.
1810 *Megachile* Latreille ; Latreille : 439.
1828 *Megachile* Latreille ; Curtis : pl. 218.
1841 *Chalicodoma* Lepeletier : 309.

GENOTYPE. *Apis centuncularis* Linnaeus 1758, selected by Curtis (1828).

REMARKS. The International Commission on Zoological Nomenclature recommended that the type-fixation (i.e. *Apis muraria* Retzius 1783) of Latreille be set aside and that of Curtis (1828) upheld (ICZN Opinion 219, 1954).

Megachile amaguensis Cockerell 1925

*1925b *Megachile amaguensis* Cockerell : 7, pl. 1, fig. 1.
1931 *Megachile amaguensis* Cockerell ; Salt : 146.

HOLOTYPE. U.S. Nat. Mus., No. 69601.

DISTRIBUTION. Tertiary : Kudia River, Siberia.

REMARKS. Cockerell states, 'The distance of the first recurrent nervure from the base of the second submarginal cell is an unusual feature, which I do not observe in living species'.

Megachile praedicta Cockerell 1908

*1908c *Megachile praedicta* Cockerell : 31.
1931 *Megachile praedicta* Cockerell ; Salt : 146.

HOLOTYPE. Cockerell Collection, whereabouts unknown.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Genus confirmed by leaves cut through as though by *Megachile.*

Megachile sp. indet. (Brischke)

1886 *Chalicodoma* Brischke : 278.
1891 *Chalicodoma* Brischke ; Scudder : 694 (5985).
1907 *Chalicodoma* Brischke ; Handlirsch : 888.
1931 *Chalicodoma* sp. Brischke ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. *Chalicodoma* Lepeletier = *Megachile* Latreille. An unnamed *Chalicodoma* was said by Brischke to occur in the Baltic amber, two specimens apparently being known to him.

Genus ***OSMIA*** Panzer 1806

*1806 *Osmia* Panzer : 230.
1810 *Osmia* Panzer ; Latreille : 439.

GENOTYPE. *Apis bicornis* Linnaeus 1758, = *Apis rufa* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. It has been found difficult to determine the identity of the species of *Osmia* known to Heer. The following notes may prove useful in clarifying this point.

In 1865 Heer mentioned 'Drei Osmien', having previously (1849) described one specimen, *Osmia antiqua,* in the Karlsruhe Collection. But quite a number of so-called *Osmia* are now in the collection at Zurich. These possess Heer's manuscript names and were actually placed by him in four groups : (1) *Osmia primaeva* ; (2) *Osmia* sp. ? *dubia* ; (3) *Osmia immortua* and (4) *Osmia kirbyana.* Which of these were the three referred to in 1865 is not known.

Cockerell (1909) studied the species *O. primaeva* (see p. 167) and referred it to *Andrena.* He did the same for *O. kirbyana* (see p. 202) and considered it, probably rightly, to be a wasp. No more '*Osmia*' examined by Heer were studied by Cockerell, except a now unidentifiable insect 9·5 mm in length.

Of the remaining two groups, those specimens labelled as *O. immortua* are unfortunately indeterminable, while of the two specimens labelled '*dubia*', one is superficially much like *immortua* and being also indeterminable it is best placed there (p. 187). The second specimen, however, is good and has been selected as the type of a new species (p. 185). However, '*dubia*', apart from being a manuscript descriptive term and not a name, is preoccupied by *Osmia dubia* (Germar). We have, therefore, named it *O. nigra.* [See also Appendix, p. 256.]

Osmia carbonum Heyden 1862

*1862 *Osmia carbonum* Heyden : 75, pl. 10, figs 11, 12.
1891 *Osmia carbonum* Heyden ; Scudder : 721 (6219).
1907 '*Osmia carbonum*' Heyden ; Cockerell : 228.
1907 *Osmia carbonum* Heyden ; Handlirsch : 889.
1936 *Osmia carbonum* Heyden ; Statz : 260.

HOLOTYPE. British Museum (Natural History), 58779 (Heyden's 1862 fig. 11).

PARATYPE. British Museum (Natural History), 58768 (Heyden's 1862 fig. 12).

OTHER SPECIMENS. Mus. Comp. Zool. Harvard.

DISTRIBUTION. Oligocene : Rott.

REMARKS. Heyden's originals were badly figured. His fig. 11 is of an insect without visible wings, and the original of fig. 12, of which the counterpart existed, was a somewhat smaller insect which has at least the more proximal portions of the wings still preserved. Both are in the British Museum (Natural History) Collection, but were badly damaged by exposure to water during the war so that no information additional to that given by Heyden can be derived from them.

On the other hand, the specimens studied by Cockerell (1907) at Harvard were 'a very good specimen with reverse' and another apparently unnamed one which may be the counterpart of the paratype. Cockerell says, 'it is evident that they were not part of Heyden's material as they do not agree with his figures and descriptions'. This is certainly true as regards his 'good specimen with reverse', but his statement relating to wingless originals of *O. carbonum* is not quite correct as far as the paratype is concerned.[3] Moreover, after mentioning the 'goodness' of the specimen with counterpart at Harvard, he later quite casually states it 'is indeterminate', a statement difficult to reconcile with others previously made. It now remains to be seen whether Cockerell's second specimen is the counterpart of Heyden's paratype. Should this prove to be the case, no change of nomenclature will be necessary. On the other hand, a significant difference will necessitate placing *O. carbonum* under the *gen. indet.* group, and a new name will be required for Cockerell's specimens.

Osmia antiqua Heer 1849

*1849 *Osmia antiqua* Heer : 95, pl. 7, figs 2a, b.
1856 *Osmia antiqua* Heer ; Giebel : 182.
1865 Drei Osmien ; Heer : 386 (*partim*).
1876 Osmiae ; Heer : 43 (*partim*).
1891 *Osmia antiqua* Heer ; Scudder : 721 (6218).
1907 *Osmia antiqua* Heer ; Handlirsch : 889.
1909c '*Osmia*' Cockerell : 316.
1938 *Osmia* Armbruster : 87.

---

[3] We consider it quite possible that the specimens described by Cockerell (1907) are, in part, the same as those described by Heyden (1862) from the collection of Dr Krantz. The difficulty of identification almost certainly lies with Heyden's poor descriptions and illustrations. That certain irreconcilable anomalies, however, do exist is quite clear, e.g. the statement that no signs of visible wings are present in a specimen of Heyden's *Apis dormitans* whereas all Cockerell's specimens of *Apis* (from Rott) possess them. In the circumstances, we have decided either to be cautious where actual similarities suggest themselves, as in *Osmia carbonum*, or to regard the two sets of material as separate and distinct, as for *Apis dormitans*.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe (Oe.91), Inv.1272.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. Cockerell (1909c) said this 'cannot apparently be referred to *Osmia* or any other genus with certainty'. He, however, never saw the type and is believed to have based his statement on Heer's (1849) entry of a specimen from the Karlsruhe Collection, and his rather poor illustration of it. Whether Heer (1865) intended this specimen to be included in his 'Drei Osmien' is not known, but it is assumed to be so.

We have now studied the type and, although not well preserved, the following characters can be discerned. Broad head with a suggestion of large compound eyes ; parts of one fore and two hind legs, the latter, on the right, possessing distinguishable hairs ; thorax well chitinized, probably not so broad as head ; abdomen also well chitinized, some segmentation visible, quite broad ; some details of wing venation can be discerned, but since hind- and forewing overlap, and parts are missing, it is only possible to state that what can be seen is not incompatible with the wing venation of *Osmia*, and certainly the character of the hind legs, segmentation of abdomen, colour, general habitus etc. do not rule out *Osmia* either.

MEASUREMENTS. Overall length, 12 mm ; breadth of head, 4·5 mm (approx.) ; breadth of abdomen 5 mm ; length of abdomen, 7 mm ; length of forewing, 9 mm.

Osmia nigra sp. nov.

(Pl. 1, figs 5, 6)

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, Pl. I, 719.

PARATYPE. Same collection, Pl. I, 685.

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. The holotype (labelled *Osmia* sp. ? *dubia*) is a comparatively small, black, insect, which is preserved in two parts, the abdomen being 5 mm distant from the head and thorax, but evidently belonging to it. The head is very imperfectly preserved but is as broad as the thorax. The thorax shows a well-developed mesoscutum. Parts of the middle and the two hind legs are preserved, and what is believed to be the hind tibia is triangular-shaped. The hind femur, however, is as strong and almost as broad as the tibia. Only the left forewing is preserved, but most of the venation can be discerned and it agrees well with *Osmia* : short, tapering marginal cell, broader at the base where it joins the pterostigma about the middle ; pterostigma well defined but not particularly large ; radial vein very strong ; two subequal submarginal cells ; basal vein short and relatively straight, of two almost equal segments, only slightly deflected at their junction ; cross-vein cu-a coincident with that of basal vein at point of juncture with Cu, but posteriorly it arches slightly proximad. Abdomen clearly reveals intersegmental membranes in the distal parts.

The paratype is an insect very reminiscent of the holotype and can be regarded as conspecific. The thorax is well developed with a broad convex mesoscutum. A middle and two hind legs are apparently preserved, with triangular tibiae. Some aspects of the abdomen are clearly shown. The specimen, however, is not generally well preserved but nevertheless corresponds with the holotype in all those characters that can be discerned except for a slightly lighter coloration. Since darker patches exist on various parts of the body, however, it is not known which was the more natural coloration for this species. No wings are preserved. Heer's manuscript name for this specimen was *Apis adamitica*, but it was clearly not the type of the latter species.

MEASUREMENTS. Holotype: length of abdomen, 6·5 mm; width, 4·5 mm; forewing length 5·5 mm (approx.). Paratype: length of abdomen 6 mm; length of thorax and abdomen (together) 10 mm.

Osmia sp. indet. (Menge)

1856 *Osmia* Menge: 26.
1891 *Osmia* Menge; Scudder: 721 (6217).
1907 *Osmia* Menge; Handlirsch: 889.
1931 *Osmia* sp. Menge; Salt: 144.

DISTRIBUTION. Eocene: Baltic amber.

REMARKS. Specimen referred to but neither described nor species determined.

Family **MEGACHILIDAE** ***incertae sedis***

'Apiaria' dubia Germar 1849

*1849 *Apiaria dubia* Germar: 66, pl. 2, fig. 8.
1856 *Osmia dubia* Germar; Giebel: 182.
1891 *Apiaria dubia* Germar; Scudder: 688 (5935).
1891 *Osmia dubia* Giebel; Scudder: 721 (6220).
1907 (*Osmia*) *dubia* Germar; Handlirsch: 889.

DISTRIBUTION. Oligocene: Orsberg bei Bonn.

REMARKS. Nothing appears to be known about this specimen. The correctness of Giebel's generic determination is very doubtful.

Megachilidae gen. et sp. indet.

MATERIAL. Eidgenössische Technische Hochschule, Zürich, Nos. Pl. I, 687 (with counterpart); Pl. I, 688 (with counterpart Pl. I, 689); X; and Pl. I, 718.

DISTRIBUTION. Miocene: Oeningen.

DESCRIPTION AND REMARKS. Two of the specimens bear Heer's MS label '*immortua*'. The specimens appear to be bees, whose known parts are not incompatible with *Osmia* but whose real systematic position cannot be satisfactorily ascertained owing to lack of diagnostic characters. The state of preservation is as follows.

(1). Pl. I, 687 (and counterpart). A fairly well-chitinized insect with head, thorax, abdomen and portion of one antenna preserved, but with almost all traces of wings effaced. Body length 10 mm ; length of abdomen 5·5 mm, width 3 mm ; length of thorax 3·25 mm, width 3 mm. Apart from segments of the abdomen few morphological details can be discerned.

(2). Pl. I, 688 and counterpart Pl. I, 689. A poorly-defined specimen, no longer with visible wing venation though the outline of the wings themselves can be detected. Tegulae quite prominent. Body length 11 mm approx. ; length of abdomen 5·5 mm, width 3·75 mm ; length of thorax not accurately determinable, width 3·25 mm.

(3). One specimen marked 'X, Hymenoptera dub.' Body chitinized, dark brown in colour and comparatively well preserved, but legs and wings completely lacking. Two well-developed compound eyes present ; thorax, though less well outlined, is featureless ; abdominal segments, five in number, clearly in evidence. Body length 10·25 mm ; length of abdomen 5 mm, width 3·25 mm ; length of thorax 3·25 mm, width 3 mm.

(4). Pl. I, 718, bearing Heer's MS label *Osmia* sp. ? (*dubia*). Head, thorax and abdomen are preserved, but legs are lacking and the wing venation is too indistinct for satisfactory recognition. Both the head and thorax are well chitinized and dark brown in colour, but the abdomen is paler. Body length (allowing for curved position) 10 mm approx. ; length of abdomen 5 mm, width 3·5 mm ; length of thorax 3·1 mm, width 3 mm (approx.).

Family **ANTHOPHORIDAE** Dahlbom 1835

Diagnosis. Labrum usually broader than long, attached by rather short margin to clypeus ; subantennal areas absent ; subantennal sutures directed towards inner margins of antennal sockets ; lower sides of clypeus frequently bent back parallel to long axis of body ; facial foveae almost always absent ; galeae elongate post-palpally, short pre-palpally ; labial palpi with first two segments elongate and flattened, first segment at least as long as second ; glossa linear, usually with a flabellum ; pre-episternal suture usually absent below scrobal suture, present above it ; middle coxae elongate, except in a few parasitic forms ; basitibial plates usually present ; scopa, when present, occurs on the posterior tibiae and basitarsi, and very rarely found on abdominal sternites as well ; pygidial area often present.

Usually three submarginal cells ; when two only, second often much shorter than first ; rarely only one closed submarginal cell.

Distribution. Eocene to Recent.

Subfamily **XYLOCOPINAE** Latreille 1802

Diagnosis. Clypeus not protuberant but relatively flat, lateral portions seen from beneath a little bent backward and more nearly transverse than longitudinal ; pygidial plate absent, represented in some females by a flat-topped apical spine which, unfortunately, is hidden in a dense pygidial fimbria and hence would be difficult to see in fossils ; scopa of female not forming a corbicula ; inner apical margins of posterior tibiae bare or hairy, without a hind tibial rake.

Michener (1944) also mentions a further distinctive feature of the clypeus of Xylocopinae, though of doubtful use for fossils. The portions of the epistomal suture between the anterior tentorial pits and the dorsolateral angles of the clypeus are subparallel to one another, while below the pits the clypeus broadens abruptly.

REMARKS. This subfamily contains two distinctive tribes, the Ceratinini and the Xylocopini, both represented by fossil forms.

Tribe **CERATININI** Latreille 1802

DIAGNOSIS. Small, rather slender bees with little pubescence ; mandibles very broad basally but abruptly narrowing to the slender, subparallel-sided apical portions ; metanotum horizontal ; apex of seventh tergum of the female produced to a small, sharp, median point.

Wing surfaces hairy throughout, not papillate ; marginal cell broad, longer than distance from its own apex to wing tip, and considerably bent from the wing margin apically ; jugal lobe of each hindwing is one-third to half as long as the anal lobe.

REMARKS. Only one fossil specimen so far known.

Genus ***CERATINA*** Latreille 1802

1802a *Clavicera* Latreille : 432.
*1802b *Ceratina* Latreille : 380.

GENOTYPE. (*Hylaeus albilabris* Fabricius 1793) = *Apis cucurbitina* Rossi 1792, by monotypy.

REMARKS. A recommendation is before the International Commission on Zoological Nomenclature that the name *Clavicera* be suppressed.

Ceratina disrupta Cockerell 1906

*1906 *Ceratina disrupta* Cockerell : 37.
1907 *Ceratina* Cockerell ; Handlirsch : 891.
1973 *Ceratina disrupta* Cockerell ; Daly : 15, pl. 2, text-fig. 4b.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2001 (= Scudder Coll. No. 9355).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. This black, average-sized bee (8 mm) has the general appearance of a *Ceratina*. Description of forewing given by Cockerell.

Tribe **XYLOCOPINI** Latreille 1802

DIAGNOSIS. Large, robust bees with coarse, plumose hair ; metanotum vertical ; apex of seventh tergum of female produced to a flat-topped spine, largely hidden in a dense mass of hair ; basitarsi fully as long as the corresponding tibiae.

Wings elongate, papillate distally ; marginal cell very slender, its apex bent away from the wing margin and the cell itself much longer than the distance from its own apex to the wing tip ; jugal lobe of hindwing much shorter than the anal lobe.

REMARKS. All fossils have been assigned to the genus *Xylocopa*.

Genus ***XYLOCOPA*** Latreille 1802

1802a *Xilocopa* Latreille : 432.
*1802b *Xylocopa* Latreille : 379.
1810 *Xylocopa* Latreille ; Latreille : 439.

GENOTYPE. *Apis violacea* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. The name *Xylocopa* has been placed on the list of *nomina conservanda* (ICZN Opinion 743).

Xylocopa friesei Statz 1936

*1936 *Xylocopa friesei* Statz : 284, 293, pl. 8, fig. 37.

HOLOTYPE. Statz Collection.

DISTRIBUTION. Oligocene : Rott.

REMARKS. Wing, thorax and hind basitarsus all strongly suggest a *Xylocopa*. According to Statz, the specimen is similar in size to *Xylocopa senilis* Heer, but since only the thorax, right forewing and four legs (two very fragmentary) are known, his statement can have but limited value.

Xylocopa hydrobiae Zeuner 1938

*1938 *Xylocopa hydrobiae* Zeuner : 127, figs 20, 21.

HOLOTYPE. Nat. Hist. Mus. Mainz, Hydrobienkalk Collection, No. 123.

PARATYPE. Same collection, No. 5.

DISTRIBUTION. Miocene : Biebrich nr Mainz.

REMARKS. Vein 2nd r-m together with distal segment of Rs is Z-shaped.

Xylocopa jurinei (Heer 1865)

*1865 *Bombus jurinei* Heer : 386, fig. 296.
1867 *Bombus jurinei* Heer ; Heer : 4, pl. 3, fig. 8.
1872 *Bombus jurinei* Heer ; Heer : 473, fig. 296.
1876 *Bombus jurinei* Heer ; Heer : 43, fig. 296.
1879 *Bombus jurinei* Heer ; Heer : 411, fig. 338.
1891 *Bombus jurinei* Heer ; Scudder : 690 (5953).
1907 *Bombus jurinei* Heer ; Handlirsch : 892.
1909c *Xylocopa jurinei* (Heer) ; Cockerell : 315.
1928 *Bombus jurinei* Heer ; Wheeler : 97.
1928 *Xylocopa* Wheeler : 97.

1931 *Bombus jurinei* Heer ; Cockerell : 301.
1931 *Xylocopa* Latreille ; Cockerell : 301.
1938 *Bombus jurinei* Heer ; Armbruster : 87.

Holotype. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 682a (Heer 1865 : fig. 296).

Other material. Same collection, No. Pl. I, 682b (Heer 1867 : pl. 3, fig. 8).

Distribution. Miocene (Sarmatian) : Oeningen.

Remarks. If the specimen No. Pl. I, 682b is not the counterpart of the holotype, a point very difficult to decide, then Cockerell (1909c) did not see the type, since his specimen was that figured by Heer (1867).

Of this specimen, Cockerell (1909c) states, 'Only part of the venation can be made out, but all that can be seen agrees with *Xylocopa,* and not with *Bombus*'. Armbruster (1938) also suggests the name *Xylocopa* for this specimen. Having examined the two existing specimens, we endorse Cockerell's conclusion as applicable to both. Moreover, the tibia and basitarsus of the hind legs bear a well-developed scopa, which is typical of *Xylocopa.* Furthermore, in specimen Pl. I, 682b, the basitarsus of the hind leg is approximately one and a half times as long as the tibia. This greater length of the basitarsus is a character of *Xylocopa,* whilst in *Bombus* the basitarsus is usually shorter than the tibia. The suture between mesoscutum and mesoscutellum is very distinct in the fossils and reminiscent of *Xylocopa.* A prominent feature of specimen Pl. I, 682b is the strong and copious hairs protruding from the apex of the abdomen, which again is observed in some *Xylocopa.*

The species is distinguished from *Xylocopa senilis* Heer by its larger size.

Measurements. Holotype : length of thorax plus abdomen, 21 mm ; length of abdomen 14 mm, width 11 mm ; length of thorax 7 mm, width 8 mm ; length of forewing 15 mm.

Specimen Pl. I, 682b : length of thorax plus abdomen 25 mm ; length of abdomen 18 mm, width 11·5 mm ; length of thorax 7 mm, width 8 mm ; length of forewing 16·5 mm. The legs here are well preserved, the length of the tibia being 3·75 mm and the length of the basitarsus 6 mm. It will also be noticed that the measurements of the thorax and the abdomen do not quite tally with those given by Heer.

Both specimens have the head missing.

Xylocopa senilis Heer 1849

(Pl. 1, figs 3, 4)

*1849 *Xylocopa senilis* Heer : 93, pl. 7, figs 1a, b, c.
1856 *Xylocopa senilis* Heer ; Giebel : 181.
1865 *Xylocopa senilis* Heer ; Heer : 386, fig. 295.
1872 *Xylocopa senilis* Heer ; Heer : 473, fig. 295.
1876 *Xylocopa senilis* Heer ; Heer : 43, fig. 295.
1879 *Xylocopa senilis* Heer ; Heer : 411, fig. 337.
1885 *Xylocopa senilis* Heer ; Scudder : 819, fig. 1109.
1887 *Xylocopa senilis* Heer ; Scudder : 821, fig. 1126.
1891 *Xylocopa senilis* Heer ; Scudder : 734 (6334).
1907 *Xylocopa senilis* Heer ; Handlirsch : 891.

1909c *Xylocopa senilis* Heer ; Cockerell : 415.
1931 *Xylocopa senilis* Heer ; Pongrácz : 117, pls (5) 7, (6) 8.
1938 *Xylocopa senilis* Heer ; Armbruster : 88.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1267.

PARATYPE. Same collection.

OTHER MATERIAL. Same collection Inv.1270 (as photographed by Pongrácz 1931 : pl. (5) 7) ; Inv.1175 (Oe.89, no. 145) ; Inv.1175 (Oe.89, no. 146) ; Inv.1228 (Oe.93). Also Eidgenössische Technische Hochschule, Zürich, no. 21a with counterpart no. 21b, and another specimen doubtfully referred here, no. 21c.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. We have studied specimens Inv.1175 (no. 145), Inv.1175 (no. 146) and Inv.1228 from Karlsruhe, and specimens 21a, b and c from Zürich. It is quite clear that we have not seen the holotype in spite of the fact that we made a thorough search for it at Karlsruhe, but we believe a photograph of it was published by Pongrácz (1931c : pl. (6) 8). The strongest evidence for this is the clear reference to the well-preserved antennae. The paratype, as defined by Heer, was 'ein sehr undeutliches Stück aus derselben Sammlung'. That we have not seen this specimen is again evident. Possibly it is the second one photographed by Pongrácz (1931 : pl. (5) 7) although the outline here is quite clear, and not indistinct as Heer suggested. Both types may now be lost but this cannot by any means be asserted since much material is still stored below the ruins of what was once the Badische Landessammlung, Karlsruhe.

In the absence of types it is difficult to know whether this is a genuine *Xylocopa* or not. At least, the specimens at Karlsruhe that have been examined are known to lack decisive detail for generic determination. The following are the measurements and characters that can be more reliably ascertained.

Inv.1175 (no. 145). Overall length 20 mm ; breadth of abdomen 8 mm ; breadth of thorax 5 mm ; length of wing on left 18 mm ; length of wing on right 14 mm. The impression of this insect is distinct and possibly a single leg is displayed on the left.

Inv.1175 (no. 146). Overall length 21·25 mm ; breadth of abdomen 8 mm ; breadth of thorax 5 mm ; length of wing on left 15 mm ; that on right 17 mm. This insect resembles no. 145, though it is not the counterpart. It is less distinctly preserved.

Inv.1228. Overall length 19 mm ; length of abdomen 12 mm ; breadth of abdomen 8 mm ; breadth of thorax 6 mm. This is a large brownish-black insect in which a few proximal veins of the wing can still be discerned, but not enough to serve any useful purpose. Very few other features are preserved.

On the other hand, the Zürich Collection contains a better preserved specimen (no. 21a, b) which shows enough of the venation of the forewing to identify it as a *Xylocopa*, the basal vein being short and the '2nd discoidal' cell (i.e. 2nd M) elongate. The copious hairs on the basitarsus of what appears to be the middle leg and the shortness of the remaining tarsal segments support this identification. Since the size agrees very well with that of *Xylocopa senilis* Heer, the specimen is assigned to this species without reservation. It is the best preserved specimen available, and has the following measurements : overall length 22 mm ; length of abdomen 12 mm, width 8–9 mm ; length of thorax 7 mm, width 9 mm ; length of forewing 8 mm. The head is rather crushed and thus of little value for measurement since it is too much spread out. The broad thorax indicates a distinct transverse suture of the notum.

Specimen no. 21c is poorly preserved, without recognizable venation. The abdomen appears to be more slender than normal for the species. Its specific and even generic identity is open to grave doubt, though it was labelled '*Xylocopa senilis* × Hr. (?)' in Heer's time. It is a smaller insect, possibly little more than 10 mm long, with a greater constriction between thorax and abdomen.

Subfamily **ANTHOPHORINAE** Dahlbom 1835

DIAGNOSIS. Clypeus almost always protuberant so that lateral portions, seen from below, are bent posteriorly and lie parallel to the long axis of the body ; the margins of the clypeus generally converge upward to the dorsolateral angles ; pygidial plate present in nearly all females and most males ; scopa of female not forming a corbicula ; anterior coxae usually little broader than long ; inner apical margins of posterior tibiae bare or hairy, without a tibial rake.

REMARKS. This very large subfamily is believed by Michener (1944) to be a monophyletic unit. The characters, however, of parasitic forms, which have evolved along different lines, are sometimes difficult to reconcile with those of non-parasitic forms, and are not always compatible with the diagnostic characters given above. The tribes Eucerini, Anthophorini and Melectini are represented by fossil forms. [See also Appendix, p. 256.]

Tribe **EUCERINI** Latreille 1802

DIAGNOSIS. Large, pollen-collecting bees ; clypeus of the male usually partly yellow or white ; antennae of males usually much elongated ; flagellar segment in the female and in some males nearly as long as the scape ; posterior legs of the male only rarely enlarged or modified ; arolia present ; scopa present ; males often possess distinct pygidial and basitibial plates.

Wing pubescent throughout and only feebly papillate apically ; marginal cell as long as, or longer than, the distance from its own apex to the wing tip, its apex narrowly rounded and bent gradually away from the wing margin ; most (including all North American) genera with three submarginal cells, the first and third longer than the second ; second abscissa of vein M-Cu of the posterior wings usually nearly twice as long as the transverse or somewhat oblique cu-a (comparable with Emphorini) and the jugal lobe about half as long as the anal lobe ; pterostigma reduced, tapering little, if at all, beyond the base of vein r.

REMARKS. The long paraglossae in the Eucerini are of doubtful diagnostic value for fossil forms. This tribe is one of the largest of the Anthophorinae but is represented with reasonable certainty by only one fossil specimen (*Tetralonia berlandi*).

Another species, *Eucera mortua*, described by Meunier (1920) has now been placed in *Anthidium*, but it is clear that Meunier felt very sure of his genus. The specimen, therefore, should be re-examined. That this was not done by us was due to our being mislead by Statz's erroneous statements (see *Anthidium mortuum* (Meunier), p. 178).

Genus ***TETRALONIA*** Spinola 1838

1810 *Macrocera* Latreille (*nec* Meigen) : 339.
*1838 *Tetralonia* Spinola : 538.

Genotype. *Eucera antennata* Fabricius 1793 (= *Apis malvae* Rossi 1790) by subsequent designation of Sandhouse (1943 : 603).

Tetralonia berlandi Théobald 1937

*1937 *Tetralonia berlandi* Théobald : 131, pl. 2, fig. 11 ; pl. 10, fig. 1.

Holotype. Museum at Marseille, Célas Collection, no. C.31.

Distribution. Oligocene, Sannoisien du Gard, France.

Remarks. This broad, black bee most closely approaches to the Recent *T. duvaucelii* Lepel., according to Théobald. It is 10 mm long, with the forewing measuring 6 mm in length. The specimen is adequately described and figured, and Théobald's figure certainly suggests an anthophorid.

Tribe **ANTHOPHORINI** Dahlbom 1835

Diagnosis. Moderate-sized to large, pollen-collecting Anthophorinae ; clypeus of male usually pale ; posterior angles of mandibles are beneath posterior margins of eyes ; first flagellar segment often elongated, sometimes as long as the scape ; scopa not large, consisting of simple, or slightly plumose, hairs, or in some cases with some plumose hairs intermixed ; claws of male cleft, of female with median tooth on inner side ; arolia mostly present ; eighth tergum of male is usually bilobed, without a pygidial plate.

Wings largely bare and strongly papillate apically ; pterostigma small, usually one and a half times as long as broad and ending at the base of vein r ; marginal cell slightly shorter than the distance from its own apex to the wing tip, rounded at its apex ; first submarginal cell, usually slightly longer on posterior margin than are the subequal second and third cells ; jugal lobe of posterior wing usually a little over one-third as long as anal lobe ; second abscissa of vein M-Cu of posterior wings about as long as cu-a.

Remarks. The genera *Anthophora* and *Anthophorites* are represented by fossil forms. The latter genus was erected by Heer (1849) for all fossil bees with affinities with *Anthophora*. The type, *Anthophorites mellona* Heer, therefore, is in need of further examination to establish its true relationship.

Genus *ANTHOPHORA* Latreille 1803

1802a *Podalirius* Latreille : 430.
*1803 *Anthophora* Latreille : 167.
1810 *Anthophora* Latreille ; Latreille : 439.

GENOTYPE. *Megilla pilipes* Fabricius 1775 (= *Apis acervorum* Linnaeus 1758), selected by Latreille (1810).

REMARKS. The International Commission of Zoological Nomemclature has recommended that the generic name *Podalirius* Latreille (1802) be rejected (ICZN Opinion 151, 1944).

Anthophora melfordi Cockerell 1908

(Pl. 1, fig. 1)

*1908b *Anthophora melfordi* Cockerell : 323.
1908d *Anthophora melfordi* Cockerell ; Cockerell : 575, fig. 6.
1931 *Anthophora melfordi* Cockerell ; Salt : 145.
1938 *Anthophora melfordi* Cockerell ; Rodeck : 295.

HOLOTYPE. British Museum (Natural History), I.9259. Counterpart in Colorado University Museum, No. 18922.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell (1908b), 'This is the first genuine fossil *Anthophora*'. The parts preserved include the head, thorax, first abdominal segment, parts of three legs, most of the forewing overlying remnants of the hindwing and the extended mouth parts.

The specimen has been re-examined and the following points noted. The forewing is well preserved, except distally. In the hindwing, however, since it is overlain by the forewing, the venation is less readily ascertainable. Some veins appear to be very badly preserved or not at all. The legs, although undoubtedly hairy, are possibly not so to the extent Cockerell suggests, nor are we able to verify his statement of the 'copious' quantity of hair on the 'tongue'.

As regards the venation of the forewing, there is no need for us to differ from Cockerell's decision to place the specimen in *Anthophora*. The juncture, however, where the first recurrent vein reaches the second submarginal cell, may be 'near the beginning of its last third instead of at the middle', but it must also be mentioned that this juncture is far from being clearly visible. Vein cu-a of the hindwing is very oblique, as Cockerell states.

Genus *ANTHOPHORITES* Heer 1849

*1849 *Anthophorites* Heer : 97.
1909c *Anthophorites* Heer ; Cockerell : 315.

GENOTYPE. *Anthophorites mellona* Heer (1849), selected by Cockerell (1909c).

REMARKS. According to Cockerell, '*Anthophorites* cannot be precisely defined, but includes various fossil bees supposed to be more or less similar to *Anthophora*'.

The genus is obviously a repository for all Anthophorid-like insects that cannot otherwise be satisfactorily determined.

The holotype of the genotypic species is now lost, but it was illustrated by Heer with some wing venation and body characters, insufficient for the establishment of a generic diagnosis. We have, however, refrained from sinking this genus because no specimens attributable to the type species have been examined by us.

Anthophorites gaudryi Oustalet 1870

*1870 *Anthophorites gaudryi* Oustalet : 104, pl. 2, figs 11, 13.
1891 *Anthophorites gaudryi* Oustalet ; Scudder : 687 (5922).
1907 *Anthophorites gaudryi* Oustalet ; Cockerell : 227.
1907 *Anthophorites gaudryi* Oustalet ; Handlirsch : 890.
1937 *Anthophorites gaudryi* Oustalet ; Théobald : 433.

HOLOTYPE. Museum at Corent, France.

DISTRIBUTION. Oligocene (Stampian) : Corent, France.

REMARKS. The specimen is poorly preserved and lacks the head. Scudder (1891) compared it with *A. parietaria*. Cockerell (1907) writes, 'has a curiously fly-like appearance', and 'its hairs are not plumose'. Oustalet's figure (1870 : pl. 2, fig. 11) is most difficult to interpret.

It should be noted that the species is not listed by Théobald (1937 : 375) where *A. mellona* is given as occurring at Corent instead.

Anthophorites thoracica Heer 1867

*1867 *Anthophorites thoracica* Heer : 6, pl. 3, fig. 14.
1891 *Anthophorites thoracicus* Heer ; Scudder : 687 (5925).
1907 *Anthophorites thoracicus* Heer ; Handlirsch : 890.

HOLOTYPE. Possibly Badische Landessammlungen für Naturkunde, Karlsruhe.

DISTRIBUTION. Miocene : Radoboj.

REMARKS. Apparently based on one specimen from Radoboj. We particularly searched for this specimen at Karlsruhe without avail. It may nevertheless still reappear when the material now stored in the cellars there is unpacked and sorted.

Anthophorites longaeva Heer 1867

*1867 *Anthophorites longaeva* Heer : 5, pl. 3, figs 12, 13.
1891 *Anthophorites longaevus* Heer ; Scudder : 687 (5923).
1907 *Anthophorites longaevus* Heer ; Handlirsch : 890.
1909c *Anthophorites longaeva* Heer ; Cockerell : 315.
1938 *Anthophorites longaeva* Heer ; Armbruster : 87.

HOLOTYPE. Heer's (1867) fig. 13 from Radoboj. Whereabouts unknown.

PARATYPE. Heer's (1867) fig. 12 from Oeningen. Whereabouts unknown.

OTHER SPECIMENS. Eidgenössische Technische Hochschule, Zürich, Nos Pl. I, 683, Pl. I, 712 and Pl. I, 809.

Distribution. Lower and Upper Miocene : Radoboj and Oeningen.

Remarks. Of the two specimens figured by Heer (1867), fig. 13, from Radoboj, appears to be well preserved. Fig. 12, from Oeningen, however, is described as 'sehr ähnlich *A. mellona*, aber beträchtlich grösser'. It is believed to have been seen by Cockerell (1909c) who described it as a bee with large eyes, narrow face, middle joints of a rather stout flagellum a little longer than broad, and an abdomen broad at the base, with fine hair ; hind tibia 3·75 mm, hind basitarsus 2·5 mm and broadened ; venation indistinguishable. The generic position of the specimen was considered by Cockerell to be 'wholly obscure'. The three Zürich specimens can be described as follows.

Pl. I, 683. A strongly chitinized insect having the head partly lacking ; thorax well outlined, but without distinct diagnostic characters ; abdomen with segments clearly indicated and covered with hairs ; hind legs poorly preserved, the basitarsus and tibia apparently hairy. Body length 16 mm ; length of abdomen 10 mm, width 5 mm ; length of thorax 4 mm, width 4 mm.

Pl. I, 712. Head, thorax and abdomen preserved, but not so highly chitinized as Pl. I, 683 ; the strong costa of the wing can be discerned ; abdomen somewhat distended ; a triangular-shaped chitinous area that is preserved may be a tibia. Length of body 17 mm ; length of head 2·25 mm ; length of thorax 4·5 mm, width 4·5 mm ; length of abdomen 10·25 mm, width 5·75 mm.

Pl. I, 809. A very weakly chitinized specimen on which few details can be discerned. Head, thorax and abdomen present, wings completely lacking and legs practically absent. Length of body 17·5 mm ; length of head 2 mm ; length of thorax 5 mm, width 5 mm ; length of abdomen 10·5 mm, width 6 mm.

These three specimens are not determinable. They are placed under this species because the characteristics that can be discerned are compatible with the holotype. They are labelled with the name *A. longaeva* in a nineteenth-century handwriting.

Anthophorites mellona Heer 1849

*1849 *Anthophorites mellona* Heer : 97, pl. 7, figs 4a–c.
1856 *Anthophorites mellona* Heer ; Giebel : 183.
1891 *Anthophorites mellona* Heer ; Scudder : 687 (5924).
1907 *Anthophorites mellona* Heer ; Handlirsch : 891.
1907 *Anthophorites mellona* Heer ; Cockerell : 229.
1909c *Anthophorites mellona* Heer ; Cockerell : 315.
1914 *Anthophorites mellona* Heer ; Meunier : 193, pl. 6, figs 5a, b, text-fig. 5.
1937 *Anthophorites melona* (Heer) ; Théobald : 375.

Holotype. Originally in Eidgenössische Technische Hochschule, Zürich, but cannot now be traced.

Other specimens. One specimen in Mus. Comp. Zool. Harvard, and another, described by Meunier, is believed to be in the Marseille Museum.

Distribution. Miocene : Oeningen. Also reported from the Oligocene of Aix and the Oligocene of Cereste, Corent, Célas, France.

REMARKS. Heer's illustration is unsatisfactory. The thorax is very hairy, and some wing venation can be made out. One specimen only was described by Heer, from the Zürich collection, where however we have not succeeded in finding it.

Cockerell (1907), while investigating specimens in the Museum of Comparative Zoology, Harvard, came across an example of *Anthophorites mellona* Heer, from Oeningen, determined by Heer himself. Its venation could not be discerned. Since, however, some wing venation must have existed in Heer's original, this specimen cannot be the holotype. Cockerell (1909c) fixed *Anthophorites mellona* as the genotype.

Meunier's (1914) specimen from Aix-en-Provence was thought by him to belong to this species, though his description was meagre. He did, however, give photographs of two specimens. His pl. 6, fig. 5a is the specimen described; it appears to be well preserved. His pl. 6, fig. 5b is probably a photograph of Heer's *A. mellona* used for comparison, although no mention of this is given. Moreover, the resemblance between the two specimens is probably merely superficial.

The reports from the Oligocene are even more doubtful. They appear in Théobald's (1937) table, for each of the three localities. There is only a single specimen, however, and one *Anthophorites* is indeed known from the Oligocene of Corent, France, viz. *A. gaudryi* (p. 195). It is listed by Théobald under that fauna (1937 : 433), but omitted from the list.

Anthophorites titania Heer 1849

*1849 *Anthophorites titania* Heer : 99, pl. 7, figs 5a, b.
1856 *Anthophorites titania* Heer ; Giebel : 183.
1891 *Anthophorites titania* Heer ; Scudder : 687 (5926).
1907 *Anthophorites titania* Heer ; Handlirsch : 891.
1909c *Anthophorites titania* (Heer) ; Cockerell : 315.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1273 (Oe.92).

PARATYPE. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 686 (not figured by Heer).

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION. The holotype has been examined, and found to have the head missing; the thorax is much distorted, and somewhat hairy. Both hind legs are in part preserved, one tibia and two basitarsi being very distinct. Both tibiae and basitarsi are broad and very hairy. The tibia is less well preserved but appears to be more than one and a half times as long as the basitarsus, without however being much broader. The abdominal segments are clearly visible and covered with long hairs. The basal vein is strongly curved at its base and soon straightens out. Length of abdomen 9 mm, width 5·5 mm.

The paratype, stated by Heer (1849) to have once been in the Karlsruhe Collection, is now at Zürich and has been examined by us. It was also studied by Cockerell (1909c) who considered its generic position to be obscure. This we hereby endorse.

The specimen is without head or legs, but the segmentation of the abdomen is clear. A few details of the thorax can be discerned : the pronotum is narrow, well margined but not quite reaching the tegulae ; the mesonotum is prominent and arched, but rather small and well defined posteriorly by a transcutal suture ; the mesoscutellum is clearly evident, the metathorax is delimited posteriorly by 'a sharp edge separating base from apical truncation', and a definite constriction exists between it and the abdomen. The wing venation has been almost effaced, but a distinct pterostigma still remains and a strong radius is present. Length of body (without head) 13·25 mm ; length of thorax 4·25 mm, width 4·1 mm ; length of abdomen 9 mm, width 5·25 mm ; length of forewing 8 mm (as near as can be ascertained).

REMARKS. The shape of the basal vein of the holotype is a trait not uncommon in *Anthophora*, as the examination of many Recent specimens has revealed. It argues strongly against the alternative of assigning *A. titania* to *Halictus*. But the characters preserved do not permit us to be certain that the species is an *Anthophora sensu stricto*.

Anthophorites tonsa Heer 1849

*1849 *Anthophorites tonsa* Heer : 99, pl. 7, figs 6a, b.
1856 *Anthophorites tonsa* Heer ; Giebel : 183–184.
1891 *Anthophorites tonsus* Heer ; Scudder : 687 (5927).
1907 *Anthophorites tonsus* Heer ; Handlirsch : 891.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. One specimen only has been described, and it cannot at the moment be found at Karlsruhe because of war damage. Heer's (1849) illustration is unsatisfactory.

Anthophorites veterana Heer 1849

*1849 *Anthophorites veterana* Heer : 100, pl. 7, figs 7a, b.
1856 *Anthophorites veterana* Heer ; Giebel : 183–184.
1891 *Anthophorites veteranus* Heer ; Scudder : 687 (5928).
1907 *Anthophorites veteranus* Heer ; Handlirsch : 891.

HOLOTYPE. Eidgenössische Technische Hochschule (Lavater Collection), Zürich, No. 14.

OTHER SPECIMEN. Same collection, No. Pl. I, 684.

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. Heer's figure of the holotype agrees well with the holotype itself except that he omits the legs although he mentions them in the text. It is not well preserved. The insect was robust, with a broad convex mesoscutum. Tegulae prominent. The hind leg, particularly the basitarsus, is hairy and as broad as the tibia. On account of a depression in the rock which crosses the tibia, the relative lengths of the tibia and basitarsus are difficult to assess. Some venation is present, but since the forewing overlies the hindwing, it is impossible to decipher it satisfactorily. The strong radius, however, is distinct and also some proximal portions of M+Cu and Cu. Length of body 14 mm; length of thorax 4·25 mm, width 5·5 mm; length of abdomen 8·75 mm, width 6·5 mm; forewing length 11 mm.

A second specimen (Pl. I, 684) labelled *Anthophorites* may tentatively be placed here. It is 12·5 mm long, extremely poorly preserved and black in colour.

Tribe **MELECTINI** Westwood 1840

DIAGNOSIS. Large, parasitic bees; clypeus of male black; posterior angle of mandible lies beneath middle of lower end of eye; first flagellar segment not unusually elongated; scopa absent; basitibial plates absent; claws with large inner basal lobe or tooth; middle tibial spurs unmodified; eighth tergum of the male usually feebly bilobate or bispinose and usually without a pygidial plate; seventh abdominal tergite of female with pygidial plate; seventh sternite of female somewhat produced, with the margins upturned to form a semitubular guide for the sting.

Pterostigma several times as long as broad, narrow, and not tapering beyond the base of vein r; marginal cell shorter than the distance from its own apex to the wing tip, broadly rounded apically, and usually not protruding beyond the last submarginal cell; normally three submarginal cells, the first usually longer than either of the others; second abscissa of vein M-Cu of posterior wings shorter than vein cu-a, sometimes virtually absent; jugal lobe of hind wing very small.

Genus ***PROTOMELECTA*** Cockerell 1908

*1908a *Protomelecta* Cockerell: 341.
1909b *Protomelecta* Cockerell; Cockerell: 81.

GENOTYPE. *Protomelecta brevipennis* Cockerell by monotypy.

REMARKS. According to Cockerell, 'A very *Melecta*-like genus but with the venation of the Eucerines and the large stigma of the Andrenids'. Special mention of the type was made by Cockerell (1909b).

Protomelecta brevipennis Cockerell 1908

*1908a *Protomelecta brevipennis* Cockerell: 341.
1909b *Protomelecta brevipennis*; Cockerell: 81.
1938 *Protomelecta brevipennis* Cockerell; Rodeck: 298.

HOLOTYPE. Univ. Colorado Mus., No. 18639.

DISTRIBUTION. Oligocene: Florissant.

REMARKS. The affinities of this species are by no means clear. It would appear to be an anthophorid, but its relationship with the melectines depends to some considerable extent on theoretical considerations only. A reinvestigation of the specimen is most desirable.

Family **ANTHOPHORIDAE** ***incertae sedis***

'Anthophora' effossa Heyden 1862

*1862 *Anthophora effossa* Heyden : 76, pl. 10, fig. 10.
1891 *Anthophora effossa* Heyden ; Scudder : 687 (5921).
1907 *Anthophora effossa* Heyden ; Handlirsch : 890.
1907 *Anthophora effossa* Heyden ; Cockerell : 228.
1936 *Anthophora effossa* Heyden ; Statz : 260.

HOLOTYPE. British Museum (Natural History), 58781.

DISTRIBUTION. Oligocene : Rott.

REMARKS. It is necessary to distinguish between the '*Anthophora effossa*' of Cockerell (1907) which appears to be an ant (p. 202), and the *Anthophora effossa* Heyden which Cockerell apparently did not see. He maintained that Heyden's figure and description did not agree with his specimen, though whether he was sufficiently indulgent towards Heyden's work in this respect is not clear. Heyden's figures, however, are entirely useless for diagnostic purposes, and the holotype was damaged during the war, so that details are no longer recognizable. A further point to be noted is the very arbitrary way in which Heyden referred his specimen to *Anthophora*. For these reasons one is left with no alternative but to place it *incertae sedis*.

Anthophoridae gen. et sp. indet. 1

1856 *Anthophora* Latreille ; Menge : 26.
1886 *Anthophora* ? Latreille ; Brischke : 278.
1891 *Anthophora* ? Latreille ; Scudder : 686 (5919).
1891 *Anthophora* ? Latreille ; Scudder : 686 (5920).
1907 *Anthophora* ? Latreille ; Handlirsch : 890.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Since Brischke had access to, and reported on, Menge's specimens, it is quite possible that Brischke refers here to Menge's *Anthophora*. Four specimens appear to have existed, though Menge mentioned only one.

Anthophoridae gen. et sp. indet. 2

1831 Hymenopt. aus der Fam. der Bienen ; Hünefeld : 2000 (i.e. 1100). (Specimens determined by Burmeister.)
1891 (Apidae) Scudder : 682 (5873).
1907 (Apidae) Burmeister ; Handlirsch : 892.
1931 Apidae, Hünefeld ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. This entry has been wrongly attributed to Burmeister. It was merely the latter's list that was used by Hünefeld.

Superfamily **APOIDEA** (except Apidae) ***incertae sedis***[4]

Apoidea gen. et sp. indet. 1

1881a Apidae ; Malfatti : 98.
1891 (Apidae) Malfatti ; Scudder : 682 (5874).
1907 (Apidae) Malfatti ; Handlirsch : 892.

DISTRIBUTION. Oligocene : Chiavone, Italy.

REMARKS. Poorly preserved.

Apoidea gen. et sp. indet. 2

1881 Apidae ; Scudder : 290.
1883 Apidae ; Scudder : 280.
1891 (Apidae – several) Scudder : 682 (5875).
1907 (Apidae – mehrere) Scudder ; Handlirsch : 892.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Scudder reported that several species occurred, 'most of them badly preserved ; the largest appears to be a *Bombus*'.

Apoidea gen. et sp. indet. 3

1907 (? Apidae) ; Handlirsch : 893.

MATERIAL. ? Hofmuseum, Vienna (Bosniaski Collection).

DISTRIBUTION. Miocene : Gabbro, Italy.

REMARKS. Poorly preserved bee with short angulated antennae, habitus related to '*Apis melisuga*' (see p. 248).

Apoidea gen. et sp. indet. 4

1895 (Apidae n.g. resembling *Eucera*) ; Scudder : 122.
1907 Apidae n.g. ? Scudder ; Handlirsch : 890.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. Some confusion exists over this entry. There are two difficulties. Firstly, according to Scudder (1895) and corroborated by Handlirsch (1907), this specimen may first have been considered a representative of *Bombus grandaevus*, but was later relegated to 'a new genus of Apidae, in which the neuration more closely resembles *Eucera*'. Secondly Cockerell (1908b) investigated a specimen, from Scudder's collection, which he referred to the genus *Calyptapis*. The doubt that arises here is whether or not Cockerell was referring to the entry of Scudder in his reference to a *Eucera* during his discussion of *Calyptapis*. See *Bombus florissantensis* (p. 212).

---

[4] See also Appendix, p. 256.

Apoidea gen. et sp. indet. 5

1928 Apidae Leach ; Pongrácz : 156.

Distribution. Miocene (Sarmatian) : Piski, Hungary.

Material. Magyar Állami Földtani Intézet, Budapest.

Remarks. According to Pongrácz, the shape of the wings and the pointed abdomen indicate *Osmia* ; the large, contiguous eyes, however, point to *Apis*. Since only the male of *Apis* has contiguous eyes, whereas the pointed abdomen is not characteristic of the male, the specimen cannot be referred to *Apis*. On account of the general unreliability of the diagnoses of Pongrácz it is impossible to say to which group of insects the fossil belongs.

FOSSILS ERRONEOUSLY CLASSIFIED AS APOIDEA

(excluding Apidae)[5]

'Formicinae' (Meunier)

*1920 *Andrena tertiaria* Meunier : 730, pl. 1, fig. 4.
1931 *Andrena tertiaria* Meunier ; Salt : 145.
1936 *Andrena tertiaria* Meunier ; Statz : 260.
1936 Formicinen ; Statz : 260.

Holotype. Heimatmuseum, Siegburg an der Lahn.

Distribution. Oligocene : Rott.

Remarks. Venation largely effaced. Statz (1936) writes : 'Nach der Bildung des Kopfes und der Fühler, sowie der Thoraxsegmentierung und dem Bau der Beine gehört das Insekt gemäss der Ansicht von Bischoff, Berlin, zu den Formicinen.' ['According to Bischoff of Berlin, this insect belongs to the formicoids on the basis of the structure of the head and antennae, as well as the segmentation of the thorax and leg anatomy.']

'Formicinae' (Cockerell) (*nec* Heyden)

1907 *Anthophora effossa* Cockerell : 228.
1907 'An Ant' ; Cockerell : 228.

Distribution. Oligocene : Rott.

Remarks. An ant, to be found among a series of specimens from Rott, in the Mus. Comp. Zool. Harvard.

Polistes kirbyanus Cockerell 1914

1909c 'Three species of *Osmia*' ; Cockerell : 316 (*partim*).
1909c A Wasp ; Cockerell : 316.
*1914 *Polistes kirbyanus* Cockerell : 638.
1914 *Osmia kirbyana* Heer MS ; Cockerell : 638.

---

[5] See also Appendix, p. 257.

Holotype. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 681, with counterpart.

Distribution. Miocene: Oeningen.

Remarks. The view is taken that among the 'three species of *Osmia*' referred to by Cockerell (1909c) as being at Zürich, one, the wasp, was called erroneously '*Osmia kirbyana*'. Not only was the generic identification wrong, but Heer appears to have given this specimen merely a manuscript name.

LARVAL CHAMBERS

'Genus' *CELLIFORMA* Brown 1934

*1934 *Celliforma* Brown : 539.
1935 *Celliforma* Brown : 527.

Diagnosis. Fossil fillings of chambers purported to have been made by unknown digging or nest-building Hymenoptera.

Genotype. *Celliforma spirifer* Brown 1934 by monotypy.

Distribution. Cretaceous to Recent.

Remarks. The name can hardly be maintained under the International Rules of Zoological Nomenclature, since it refers to objects made by animals, not to the animals themselves. It is used by Brown merely for the sake of convenience, in conformity with the practice adopted in palaeontology for fossil burrows, worm casts and footprints.

Celliforma favosites Brown 1941

*1941a *Celliforma favosites* Brown : 54, pl. 1, figs 1, 2.
1941 *Celliforma favosites* Brown ; Bequaert & Carpenter : 51.
1941b *Celliforma favosites* Brown ; Brown : 105.

Holotype. U.S. Geological Survey Collection.

Distribution. Upper Cretaceous, Colorado and Montana Beds: Gunlock, south-west Utah, U.S.A.

Remarks. Regarded by Brown as the comb of a wasp's nest resembling that of *Polistes*, but the possibility that it belongs to a social bee cannot be entirely dismissed. Bequaert & Carpenter (1941) questioned the correctness of Brown's determination, to which Brown (1941b) appears to have satisfactorily replied.

Celliforma spirifer Brown 1934

1934 Upper Eocene fossil molds ; Brown : 534, fig. 3.
*1934 *Celliforma spirifer* Brown : 539.
1935 *Celliforma spirifer* Brown ; Brown : 527.

Holotype. U.S. Geological Survey Collection.

Distribution. Eocene, Bridger Formation: Wyoming, U.S.A.

REMARKS. This cell resembles that of an *Anthophora*, with a rounded base and a spiral seal. Brown, however, emphasizes that many anthophorid bees construct such cells, hence little systematic significance can be attached to these features, except that they render probable the existence of Anthophoridae or similar bees.

Celliforma germanica Brown 1935

1907 *Anthophora* (*Podalirius*) ? sp. Schütze : 25, pl. facing p. 56, figs 22, 23.
*1935 *Celliforma germanica* Brown : 527.

LECTOTYPE. Württembergische Naturaliensammlung, Stuttgart (Schütze's fig. 22), here selected.

OTHER SPECIMENS. Same collection, Schütze's fig. 23, and a third specimen referred to on p. 26.

DISTRIBUTION. Oligocene, Bunter Breccia : Wilheim, Ries, Württemberg.

REMARKS. Schütze recognized these as burrows of Hymenoptera, and thought they belonged to a species of *Anthophora*, but it is impossible to assign them to any particular genus. It should be noted that they differ from *C. spirifer* and *C. nuda* in the presence of a slight waist-like constriction. A spiral lid is not preserved.

Celliforma nuda Brown 1935

1915 *Lithophaga nuda* Dall : 129, pl. 24, fig. 4.
1934 Lower Miocene fossil molds ; Brown : 534, fig. 1.
*1935 *Celliforma nuda* Brown : 527.

HOLOTYPE. U.S. Nat. Mus., No. 165187 or 165189 (Dall 1915 : pl. 24, fig. 4).

DISTRIBUTION. Lower Miocene, Silex beds of Tampa Limestone : Florida, U.S.A.

REMARKS. Originally described (Dall 1915) as molluscan boreholes, but recognized by Brown (1935) as hymenopterous. Dall had both molluscan shells of a *Lithophaga nuda* which he had described previously, and also burrows which he assigned to this species. Brown rightly identified as hymenopterous the burrow-filling figured by Dall ; hence it is the holotype of a species *Celliforma nuda* Brown (*nec* Dall).

The cell resembles that of *C. spirifer* Brown in its structure, including the spiral lid.

Celliforma bedfordi sp. nov.

(Pl. 1, figs 7, 8)

DIAGNOSIS. The innermost surface of the seal, that facing the main chamber, is distinctly spiral in structure, of at least five whorls, and is markedly concave.

HOLOTYPE. British Museum (Natural History), In.31434.

TYPE LOCALITY. Venus Bay, South Australia.

DISTRIBUTION. Pleistocene or Sub-Recent, calcareous travertine and consolidated dune-rock, coasts of south and west Australia.

REMARKS. Specimens of these chambers were obtained, in 1933, by the British Museum (Natural History) from Mr R. Bedford of Kyancutta Museum, South Australia. They differ from those described by Lea (1925) in that they are tubular, with septate cross walls, some 6–7 cm long by 2 cm in diameter. According to the correspondence of Mr Bedford, 'the prevalent type is only the main chamber of a structure of which the missing portion consists of a considerable number of small chambers separated by concavo-convex septa'. The latter, however, are believed to be the various layers of a single seal to the main chamber.

Celliforma septata sp. nov.

(Pl. 1, fig. 9 ; Pl. 2, fig. 1)

DIAGNOSIS. The innermost surface of the seal, facing the main chamber, is a plug which is not spiral. It appears to be just slightly convex. Seal composed of four septa.

HOLOTYPE. British Museum (Natural History), In.31435.

PARATYPE. Same collection, In.34133.

TYPE LOCALITY. Venus Bay, South Australia.

DISTRIBUTION. Pleistocene or Sub-Recent, calcareous travertine and consolidated dune-rock, south and west Australia.

REMARKS. These chambers appear to correspond to *C. bedfordi* n. sp. in size and shape, but differ in the form of the seal.

Celliforma sp. indet.

1932 'Tubular burrows in natural chalk' ; Buxton : 3.

DESCRIBED SPECIMEN. British Museum (Natural History), Dept. of Entomology.

DISTRIBUTION. ? Bronze Age, not later than King Solomon, Megiddo, Palestine.

REMARKS. Perhaps made by *Osmia* or *Anthophora*, according to Buxton (1932). No seal described. A second group of 'mud nests', submitted by Mr P. L. O. Guy, Oriental Institute, Chicago University, was also mentioned by Buxton. This appears to be a group of puparia reminiscent of the Australian forms described by Lea (1925), but somewhat smaller and made of different material. The latter were reasonably assumed to be the work of beetles still living in the vicinity. No such conclusion can be hazarded of the organisms responsible for the 'mud nests' of Megiddo.

'Genus' ***URUGUAY*** Roselli 1939

Uruguay auroranormai Roselli 1939

*1939 *Uruguay auroranormai* Roselli : 73, figs 17–20, 22, 31(1–4).
1941 *Uruguay auroranormai* Roselli ; Bequaert & Carpenter : 53.
1941b *Uruguay auroranormai* Roselli ; Brown : 110.

Distribution. Cretaceous or later : Uruguay.

Remarks. Unfortunately the original work in which Roselli described the hymenopterous cells has not been seen, but it is fairly obvious that Bequaert & Carpenter's comparison of Brown's Cretaceous fossil, *Celliforma favosites* (p. 203), with *U. auroranormai* is far-fetched. It would appear from the descriptions of Bequaert & Carpenter (1941) and Brown (1941b) that the cells are not dissimilar to those described in the present work from south and west Australia and may well be the work of bees. Moreover, as Brown has pointed out, the fact that they occur in Cretaceous strata does not imply a Cretaceous origin for them.

V. SYSTEMATIC DESCRIPTIONS OF FOSSIL APIDAE

This section contains a detailed study of the fossil Apidae. The material is arranged according to tribes, and within them stratigraphically.

Family **APIDAE** Latreille 1802

Diagnosis. Social bees, except possibly the tribe Euglossini (which has not so far been found in the fossil state) ; second flagellar segment much shorter than scape ; basitibial plates absent ; scopa of female, when present, forming a corbicula on each posterior tibia, except in queens of Meliponini ; inner apical margins of posterior tibiae of non-parasitic females, except in queens of Meliponini and workers of *Lestrimelitta,* provided with a tibial pollen rake ; pygidial plate absent ; wings hairy throughout, except possibly in a few fossil forms ; usually (and in all North American forms) the distance between the costal ends of the two recurrent veins is nearly twice as great as the length of the second recurrent vein, or even more, and is longer than the first recurrent.

CHALCOBOMBUS Group

Many fossil insects carry characters of such a type that their exact systematic position is difficult to define. Often new families, subfamilies and tribes are created for them but not infrequently this procedure defeats its own end by establishing units of separation where none exist. *Chalcobombus* embraces such a group and it seems to us inadvisable to erect a new tribe for it. This genus could be regarded as having affinities with the Bombini, or else it may have been the progenitor of *Sophrobombus* which we consider to be an ancestral Meliponine, and thirdly, it is not without affinity with the genus *Electrapis* which links it with the Apini. For these reasons we have not assigned a tribal name to the genus.

Genus ***CHALCOBOMBUS*** Cockerell 1908

*1908b *Chalcobombus* Cockerell : 327.
1909d *Chalcobombus* Cockerell ; Cockerell : 12.

Genotype. *Chalcobombus humilis* Cockerell 1908, by subsequent designation of Cockerell (1909d : 11).

Description. Apidae of compact build, about 8 mm long; metallic tints sometimes in evidence; head broad, vertex usually with coarse, erect bristles, sparingly plumose, facial quadrangle variable; eyes not usually hairy, and ocelli large, close together, in a slight curve; scape comparatively long, flagellum variable in size; mouth parts elongate, 'tongue' hairy but slender with an apical circular flabellum; mandible with at least two marginal notches; abdomen subglobose; scutellum prominent and hairy; legs hairy, hind ones considerably plumose, pulvillus large, claws with short inner tooth; antenna cleaner with exceptionally long hairs, lining the notch or 'auschnitt', its clasp unusually large, fringed with very fine hairs along its inner surface, lacking a lobe, variable in size; along the distal margin of the hind tibia a crude rake of strong stiff setae, and flanking its anterior margin an inner tibial spur with one edge of stiff hairs, closely set. This spur is fairly closely pressed against the legs.

Forewing. Stigma distinct, slightly variable in size, triangular; marginal cell deepish, not particularly long; three subequal submarginal cells, the first sometimes the largest, but all three exhibiting variations in shape that are of specific value; second submarginal cell receiving first recurrent nervure beyond or near the middle; third submarginal cell receiving second recurrent nervure a short distance from its end; junction of cubito-anal cross vein and basal nerve coincident.

Hindwing. Cross vein cu-a somewhat oblique, or the upper half vertical; hamuli variable in number (8–11).

Remarks. The genus was only mentioned in 1908 in a list of *Chalcobombus* species and in a genealogical tree. It was fully described in 1909. The above description is based entirely on Cockerell's published papers.

Chalcobombus hirsutus Cockerell 1908

*1908b *Chalcobombus hirsutus* Cockerell: 326.
1909d *Chalcobombus hirsutus* Cockerell; Cockerell: 12, text-fig. 8.

Holotype. Geological Museum, University of Koenigsberg.

Distribution. Eocene: Baltic amber.

Diagnosis. Head and thorax with long whitish hairs.

Description. A compact black bee, 8 mm long; head and thorax, particularly the scutellum, with long, white or yellowish hairs apparently intermixed with brown ones, and all sparingly plumose; face, particularly below, broad; scutellum conspicuously projecting; wings reddish-fuliginous; distal corner of second submarginal cell produced, third submarginal cell longer than second, narrowed more than half above.

Basitarsus as in *C. humilis*; legs with much coarse fuscous hair; flagellum is given as about 0·255 mm long and 0·170 mm thick, last joint 0·323 mm long.

Remarks. This species was first listed with characters in 1908, but not fully described until 1909.

Chalcobombus humilis Cockerell 1908

*1908b *Chalcobombus humilis* Cockerell : 326.
1909d *Chalcobombus humilis* Cockerell ; Cockerell : 12, text-figs 6, 7.
1931 *Chalcobombus humilis* Cockerell ; Salt : 145.

HOLOTYPE AND PARATYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene : Baltic amber.

DIAGNOSIS. Head and thorax above with short, black hair.

DESCRIPTION. Black, about 8·5 mm long ; head and thorax above with short, black hair ; vertex and front dull, with sparse, short, coarse, erect, black bristles, sparingly plumose ; second 'antennal joint' barrel-shaped ; wings dark fuliginous ; stigma triangular and distinct, marginal cell ending rather obtusely away from costa and possessing a small appendiculation ; second submarginal cell greatly narrowed above, narrower on marginal than is the third ; third submarginal cell narrowed at least half above.

Basitarsus squarish ; flagellum a little variable in size and possibly in thickness – Cockerell quotes lengths of 1·955 mm and 2·125 mm, and thickness 0·187 mm.

REMARKS. This species, selected by Cockerell (1909d) as the genotype, was first listed with characters in 1908 but not fully described until 1909.

Chalcobombus martialis Cockerell 1908

*1908b *Chalcobombus martialis* Cockerell : 326.
1909f *Chalcobombus martialis* Cockerell ; Cockerell : 22.
1931 *Chalcobombus martialis* Cockerell ; Salt : 145.

HOLOTYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene : Baltic amber.

DIAGNOSIS. Head, mesothorax and scutellum dull black, prothorax and tubercles coppery red.

DESCRIPTION. About 8 mm long ; mesothorax, scutellum and vertex dull black, but prothorax and tubercles coppery red ; face and abdomen black but legs metallic copper-red or crimson, moreover, the hind margins of the segments very narrowly but conspicuously silvery white, the dark part next to the margins stained with red, especially on the first segment ; scape shortish ; hind basitarsus twice as long as broad ; third submarginal cell is broad above ; first recurrent nervure joins second submarginal cell near middle ; wings pale reddish brown ; stigma large but not of great width ; second recurrent nervure with strong double curve.

Thick-set bee ; pubescence black or dark fuscous, not abundant ; the antennal joints appear to be known with some precision, as follows : third longer than second, fourth very short, about twice as broad as long, fifth conspicuously longer than fourth.

REMARKS. This species was listed with characters in 1908, but not fully described until 1909.

Tribe **BOMBINI** Latreille 1802

Diagnosis. Moderate-sized to large hairy bees; clypeus slightly protuberant, its lower lateral portions being slightly bent backward; malar space long; labrum about twice as broad as long; proboscis usually not reaching beyond middle coxae; scutellum rounded; posterior tibiae of male neither swollen nor fossate; two posterior tibial spurs always present; pterostigma often small, not tapering beyond base of vein r; apex of marginal cell separated from wing tip by a distance equal to at least half of cell; jugal lobe of hindwing becoming reduced or absent.

Remarks. No primitive forms are known of this tribe, the earliest appearing in the Oligocene (Aquitanian), and these are poorly preserved. The first convincing bumble bees are of Oligocene age, from Florissant. [For *Probombus* see Appendix, p. 256.]

Genus ***BOMBUS*** Latreille 1802

*1802a *Bombus* Latreille : 437.
1906 *Calyptapis* Cockerell : 42 (Genotype *Calyptapis florissantensis* Cockerell 1906 by monotypy).
1908b *Calyptapis* Cockerell ; Cockerell : 324.

Genotype. *Apis terrestris* Linnaeus 1758 [ICZN Opinion 220, 1954].

Diagnosis. Moderate-sized to large hairy bees; clypeus slightly protuberant; female with well-developed corbicula on each hind tibia, the latter also possessing two strong spurs but no developed comb.

Basitarsus rectangular, strongly developed and inner surface covered with strong coarse bristles; depstum or auricle present. Posterior tibia of male flattened but without corbicula.

Bombus crassipes Novak 1877

*1877 *Bombus crassipes* Novak : 92, pl. 3, fig. 4.
1891 *Bombus crassipes* Novak ; Scudder : 690 (5951).
1907 *Bombus crassipes* Novak ; Handlirsch : 891.
1928 *Bombus crassipes* Novak ; Wheeler : 97.
1931 *Bombus crassipes* Novak ; Cockerell : 309.
1936 *Bombus crassipes* Novak ; Statz : 260.

Holotype. Whereabouts unknown.

Distribution. Oligocene (Aquitanian) : Krottensee, Bohemia.

Description. Length of body 10 mm, width 6 mm; dark brown in colour, densely hairy; hind legs strongly developed, very hairy; auricle possibly not so well developed; femurs of hind legs thick; tibiae flat, widening posteriorly and truncated; basitarsus large, flat and truncated at both ends.

Remarks. One specimen only, not well preserved, neither head nor wings being discernible. Fortunately Novak's description is helpful. It suggests that the specimen was a genuine *Bombus*. The figure, however, is very bad and possibly incorrect since three hind legs are displayed. What may be the right hind leg is in the correct position, and except for the omission of the auricle and the tibial spurs is remarkably reminiscent of *Bombus*. Of the left hind leg, the basitarsus only is satisfactorily preserved. This, too, is *Bombus*-like. The third 'leg' is depicted in an anterior position where in fact the wing might be expected ; perhaps only a mass of chitin is intended, which has been given the semblance of a basitarsus by the artist. The hind leg is very hairy and the corbicula is clearly indicated.

Bombus abavus Heer 1867

(Pl. 2, fig. 2)

*1867 *Bombus abavus* Heer : 5, pl. 3, figs 9, 10.
1891 *Bombus abavus* Heer ; Scudder : 690 (5948).
1907 *Bombus abavus* Heer ; Handlirsch : 892.
1909c *Xylocopa abavus* (Heer) ; Cockerell : 314.
1928 *Bombus abavus* Heer ; Wheeler : 97.
1928 *Xylocopa abavus* (Heer) ; Wheeler : 97.
1931 *Bombus abavus* Heer ; Cockerell : 309.
1931 *Xylocopa* Cockerell : 309.
1938 *Bombus abavus* Heer ; Armbruster : 87.

Holotype. Said to be in Eidgenössische Technische Hochschule, Zürich, but no trace can be found in that collection, and it must be presumed lost.

Material. Two specimens in the Eidgenössische Technische Hochschule, Zürich (Nos. Pl. I, 808, examined by Cockerell, and SN.201) ; one specimen in the Badische Landesammlung für Naturkunde, Karlsruhe (No. Inv.1268) (Oe.90)).

Distribution. Miocene, Oeningen.

Description and Remarks. Cockerell and Armbruster, who did not examine the type, were inclined to place this species in *Xylocopa*, possibly because of Heer's remark that the basitarsus is hairy. The venation, however, which Cockerell wrongly maintained could not be made out, is somewhat like that of *Bombus* in specimen No. Pl. I, 808. Moreover, the 'globular' abdomen of specimen SN.201 is not a feature of *Xylocopa*. In the circumstances it is advisable to retain this form in the genus in which it was originally placed, but its systematic position remains uncertain. The three existing specimens may be described as follows.

Specimen Pl. I, 808. Only thorax and legs are preserved with parts of the wings, especially the greater part of one forewing. The basal vein is fairly long, and its posterior segment is much longer than its anterior segment ; cross vein cu-a is slightly distad of junction of basal nerve with Cu ; second recurrent nerve is angular shortly before it meets the base vein of the second submarginal cell. The last recurrent nerve is incompletely preserved, and the junction lies in the proximal half of this vein.

The wing differs from that of *Xylocopa* in that the anterior segment of the basal vein, although short, is not so short as is usual for this genus, secondly in the comparatively slightly greater length of the basal vein, and thirdly in the fact that the second recurrent nerve meets the base vein of the second submarginal cell well away from its apex. In these characters it resembles *Bombus*.

Forewing length at least 6·5 mm. The legs,[6] particularly the hind ones, are stout and hairy but not so much as to warrant the exclusion of the species from *Bombus*. The broad thorax reveals substructures of the notum, which was not without hairs. Length of thorax 4 mm, width 5·5 mm.

Specimen SN.201. Head not preserved. The fossil consists of thorax and abdomen with parts of legs, and the merest trace of a wing. The thorax and abdomen are hairy and there is a strong suggestion of hairs on the legs. Since the type figured by Heer indicated an insect which had part of the head and several legs present, it is obvious this is not Heer's type. Length of thorax 4 mm, width 5 mm; length of abdomen 6 mm.

Specimen Inv.1268 (Oe.90). This specimen was identified on the label as *Xylocopa senilis*. Like the other known fossils referred to this species (p. 191) it is poorly preserved, lacking head, part of thorax, and all legs except one hind femur and tibia. The abdomen, however, is complete, and the hairs and segmentation very distinct. Moreover, wings are present, that on the right showing some important features of the venation. Dimensions: length of abdomen 10·5 mm, width 7 mm; length of forewing 10 mm; length of hind tibia 3·5 mm. It is thus clear that the specimen is larger than the other known specimens of *B. abavus*, but since bumble bees vary much in size, this is no reason for excluding it from the present species.

Diagnostic characters are seen in the shape of the marginal cell, particularly in the concavity of its base, which in *Xylocopa* is convex and very acute proximally, in the position of the insertion of the first submarginal cross vein (abscissa Rs) on the posterior margin of the marginal cell which is much more distal in *Xylocopa*, and also in the curve, or rather indentation, of the cubitus just prior to its distal splitting into Cu_1 and Cu_2, a character much less prominent or lacking in *Xylocopa*. These are not conclusive arguments for placing the specimen in the genus *Bombus* rather than *Xylocopa*, but since in addition the long tibia has strong hairs arranged in a manner suggesting a corbicula, the evidence becomes overwhelming. That femur and tibia are preserved, rather than tibia and basitarsus, is proved by the angle between them. The basitarsus, indeed, is present also but only very incompletely preserved; superficially it resembles the distitarsi. Its erroneous interpretation as distitarsi no doubt contributed to the earlier identification of the specimen with *Xylocopa*.

The colour of the chitin and hairs is dark brown. Hairs are very conspicuous on the apex of the abdomen but become much sparser on the base of the abdomen and the thorax. Markings on the thorax indicate the presence of morphologically distinct regions, but these are too poorly preserved to be of use for generic identification.

---

[6] Cockerell (1931) maintained, 'The legs show a scopa, and the hind tibia is very broad, with a gently curved longitudinal ridge visible on both sides, and, therefore, certainly natural. This ridge is normal for *Xylocopa*, to which *Bombus abavus* Heer must apparently be referred'. This ridge, however, could quite well, in part, be the outline of the corbicula of a *Bombus*, and in any case would almost certainly have been masked by the scopa in a fossil *Xylocopa*.

Bombus florissantensis (Cockerell 1906)

1895 Apidae n.g. ; Scudder : 122.
*1906 *Calyptapis florissantensis* Cockerell : 42.
1907 *Calyptapis florissantensis* Cockerell ; Handlirsch : 890.
1908b *Calyptapis florissantensis* Cockerell ; Cockerell : 324, 326.
1909b *Calyptapis florissantensis* Cockerell ; Cockerell : 80.
1931 *Calyptapis* Cockerell ; Cockerell : 311.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2008 (= Scudder Coll. No. 4933).

MATERIAL. Specimen studied by Cockerell (1908), from the Oligocene shales of Florissant.

DISTRIBUTION. Oligocene : Florissant.

DIAGNOSIS. Length of body 15 mm ; length of anterior wing 8·5 mm ; head and thorax black but abdomen rather pale reddish, the junctions of the segments distinguished by moderately broad, light bands ; although legs are hairy, as in *Bombus*, and the hind legs exhibit a corbicula, the abdomen is not noticeably hairy, and the inner tooth of the bifid claws is much smaller and shorter.

Wings hyaline, with pale veins, cubito-anal cross vein (cu-a) of forewing vertical except where it bends away immediately prior to the junction with basal nerve. It differs from Recent *Bombus* 'in the form of the third submarginal cell and in the somewhat less specialised second submarginal' (Cockerell 1908b).

Stout-bodied, like Recent *Bombus* ; hind basitarsus flattened and quadrate, with hairy margins. It is stated to be 'broadly emarginate apically'.

REMARKS. The above description is based on Cockerell's of 1908. He placed the specimen in the genus *Calyptapis* because of the peculiarities of the second and third submarginal cells. Apart from the vagueness of his statement, however, it is precisely at this part of the wing that variation might be expected in an Oligocene species. The erection of a new genus indeed appears to confuse the issue, for it seems to us that we are here dealing with a perfectly legitimate *Bombus* able to bear the most detailed comparison with Recent forms.

Formerly Cockerell regarded it as near *Melissodes* (Anthophoridae), but since 1908 as one of the Bombini. He apparently based his first description on a poorly preserved specimen already referred to *Eucera* by Scudder (1895), who said it was 'an insect which may possibly be *Bombus grandaevus* Heer, but which belongs to a new genus of Apidae, in which the neuration more closely resembles that of *Eucera*'. Later, a better specimen was discovered which clearly indicated the relationship with *Bombus*.

Bombus proavus Cockerell 1931

*1931 *Bombus proavus* Cockerell : 309, pl. 1, fig. 8.
1936 *Bombus abavus* Cockerell ; Statz : 295.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2940a, b.

DISTRIBUTION. Miocene, Latah Formation ; near Spokane, Washington, U.S.A.

Diagnosis. A robust insect, with long black hair, at least on the face; forewing 15 mm long; basal vein slightly proximal of junction of vein cu-a; first submarginal cross vein (abscissa Rs) not angulate; first marginal cell on first media cell slightly longer than second submarginal on same cell; second submarginal cell on the marginal cell very little longer than the third on same cell; lower side of third submarginal conspicuously bent at insertion of second recurrent; wing hyaline, slightly brownish, the upper part of the marginal cell moderately infuscated.

Remarks. Insect known from Cockerell's description and figure. Its body is so crushed that most features are obliterated, but the forewing is in an excellent state of preservation. As with *B. florissantensis* (Cockerell) the third submarginal cell in this specimen differs from Recent *Bombus*.

According to Cockerell this was the first true fossil *Bombus* to be described, and all other species belong to other genera or are of doubtful reference to *Bombus*. He also maintains that it is 'nearest to European *B. lapidarius*'. Statz (1936) when referring to this specimen erroneously named it *B. abavus*.

Tribe **MELIPONINI** Handlirsch 1924

Description. Moderate-sized to minute bees, in perennial colonies; Recent forms with eyes bare, sparsely hairy in some queens; labrum much broader than long; epistomal suture arched upward, as in *Apis*, close to the antennal sockets, and the clypeus not protuberant.

Posterior tibial spurs reduced or absent; tibial comb always present in Recent forms (*Lestrimelitta* excepted) and distinct; in fossil forms if a comb is not present there is always an inner but modified tibial spur. Basitarsus very rarely as broad as tibia; auricle or true depstum apparently always absent, while the inner surface of the basitarsus may not have the whole area completely covered with strong bristles; claws of Recent females simple.

Ninth sternum of male virtually absent, being represented, if at all, by a narrow, longitudinal, weakly sclerotic band beneath the genitalia; eighth sternum rather narrow, having the form characteristic of the ninth in most bees; sting reduced.

Wings extending beyond the body; marginal cell often open, and forewing with veins always weak (or weakening) distally; pterostigma of moderate to large size, extending well beyond base of vein r; jugal lobe of hindwing present.

Remarks. The genus *Sophrobombus* is represented by fossil forms, but not *Melipona*. The tribe ranges from Eocene to Recent and is today widely distributed in the tropics. Many are found in East African copal.

Genus ***SOPHROBOMBUS*** Cockerell 1908

*1908b *Sophrobombus* Cockerell: 327.
1909f *Sophrobombus* Cockerell; Cockerell: 21.

Genotype. *Sophrobombus fatalis* Cockerell 1908, by monotypy.

Diagnosis. Small bees resembling *Chalcobombus* ; mandibles with at least a convex cutting edge ; ocelli large and arranged in a curve.

Basitarsus flattened, quadrangular, short, having on the inner surface a small, bristleless area around the posterior apex ; a ridge of short hairs exists on the inner surface of the hind tibia ; inner hind tibial spur present, fringed with hairs along one edge, and acting as a 'stop' to the pollen rake.

Forewing with second submarginal cross vein absent ; basal vein going basad some distance from vein cu-a ; pterostigma well developed ; marginal cell possibly slightly open at apex.

Remarks. Cockerell considered this genus to be a near descendant of *Chalcobombus*. It differs from it, however, in a number of points, particularly in the reduction of the wing venation. In this respect it is much nearer *Trigona* which it closely resembles in habitus, as well as in the hairless patch on the inner surface of the basitarsus and the ridge on the inner surface of the hind tibia. There seems little doubt therefore that it could have been an ancestor of the Meliponini. The presence of the inner tibial spur, rather than hindering this view, fosters it.

The genus was first mentioned by Cockerell (1908) in a list of Baltic amber species and in a genealogical tree. It was fully described in the following year.

Sophrobombus fatalis Cockerell 1908

(Pl. 2, figs 3, 4)

*1908b *Sophrobombus fatalis* Cockerell : 326.
1909f *Sophrobombus fatalis* Cockerell ; Cockerell : 21.
1931 *Sophrobombus fatalis* Cockerell ; Salt : 146.

Holotype. Geological Museum, University of Koenigsberg.

Material. Scheele Collection, No. 1225, in Geologisches Staatsinstitut, Hamburg.

Distribution. Eocene : Baltic amber.

Diagnosis. Length 8–8·5 mm. Short, thick-set insect, metallic dark coppery-red, almost without pubescence. Vertex with very short fuscous plumose hair. Mandibles broadened apically, with a convex cutting edge ; clypeus weakly punctate ; scape comparatively long and curved. Thorax above with erect, strongly plumose fuscous hair, twice as long on scutellum as on mesothorax ; scutellum projecting. Hind tibia long and large ; hind basitarsus quadrangular, less than twice as long as broad, the outer angles acute. Claws with an inner tooth a little beyond the middle.

Description. Cockerell gave the following description of the specimen : 'Mandibles (apparently without visible teeth) with long and short bristles on the lower margin ; blades of maxillae long and slender ; antennae very much closer together than either is to the eye, second joint barrel-shaped, but its basal third narrower and cylindrical, third joint much longer than fourth but not quite so long as second, fourth broader than long ; legs moderately clothed with fuscous hair ; pulvillus large ; 2–4 tarsal joints, small, cordiform ; wings pale fuscous, veins and stigma dark brown ; hind wing with vein cu-a a little oblique, with the lower endmost apicad.' We have examined specimen no. 1225 and find that it agrees closely with the above description, except that the second flagellar joint, i.e. third antennal joint, is somewhat longer than the first. This does not, however, justify creating a new species. The detailed description of this new specimen is as follows.

A metallic, coppery-red insect, not hairy. Overall length, from head to wing tip, 8·5 mm ; the actual body, however, is shorter, with an overall length from head to the tip of the abdomen of only 6 mm. The extent of wing overlap is thus considerable but was possibly somewhat less in the living creature since the whole abdomen is compact, which suggests considerable contraction. Other approximate measurements are : width of thorax 2·75 mm, length 2·5 mm ; width of head 2 mm, length 1·25 mm ; length of tibia 2·5 mm.

Head. The rather large head is not preserved in its entirety since a hollow occurs in the amber near the mouth parts, and some 'schimmel' also has developed here. The upper part, however, is distinct. The compound eyes appear to be naked ; the vertex is covered with fuscous hair, possibly plumose ; ocelli are large and prominent, set in a broad shallow triangle ; malar space quite broad but short, if the limits of observations are the actual limits of this region ; one antenna quite distinct, inserted on the lower half of the face ; scape well formed, curved ; basal segment of flagellum, i.e. the pedicel, barrel-shaped, second slightly larger than first, but tapering basally, third the shortest, broader than long but not much shorter than the fourth segment, the terminal segment the largest, at least twice the size of the remaining segments which are equal in shape and size. Eleven flagellar segments are present.

Thorax above indistinct owing to cracked amber and some 'schimmel'. It was apparently well arched and covered with hairs which extended somewhat down the sides. The projected scutellum can be observed.

Abdomen. Ovoid in shape. Although the tip of the abdomen can be seen very distinctly, there is no trace whatever of a sting.

Legs. Only the hind legs have been sufficiently preserved for study. They are remarkable for the great length of the tibia with a shallow scoop-like extension overlapping the base of the basitarsus on the outside, and the comparatively small, quadrangular basitarsus, not much longer than broad, with the posterior distal angle strikingly acute. In detail, the hind leg has the following characters.

Tibia. Corbicula present with the usual scopa, some hairs of which may be slightly plumose ; the corbicula itself relatively free from hairs ; the inner surface of the tibia exhibits, posteriorly, a longitudinally arranged plateau-like region of short close hairs, occupying a third of its area and extending slightly to the femur, and bounded (though seen only under certain lighting conditions) by a dark rim which is quite broad towards the base of the femur but narrow on the tibia except for a broader zone at the pollen rake. Two appendages are to be found on the tibia, a strong pollen rake and an inner tibial spur, the latter having become modified to carry a blade of fine hairs, as though developing into a comb. That it is not the latter is clear from its position on the inner surface of the tibia where it forms a 'stop' to the pollen rake. It also differs from the typical spur by being more closely pressed against the leg and more intimately associated with the pollen rake.

Basitarsus. The inner surface exhibits a well-developed pollen brush, consisting of seven rows of strong bristles, with possibly 18–20 bristles to the middle rows, though the latter number is difficult to ascertain with complete accuracy owing to pollen clogging the brush. Apical and basal rows have at least four bristles less in consequence of the development of small, bristleless areas around the posterior apices.

Pulvillus large ; claws bulbous at base and strong, with very small tooth beyond half-way ; remaining tarsal joints cordiform.

Wings. Fuscous, hairy, and rather more elongate than is normal for the Baltic amber bees. A study of the venation of the forewing reveals the absence of the second cross vein of the submarginal cells ; the basal vein becoming basad a short distance away from vein cu-a ;[7] the latter vein a little oblique, the posterior end most apicad ; stigma well developed ; marginal cell pointed ; second submarginal cell shorter than slightly open marginal ; second recurrent vein weak and sloping strongly basad. Since the forewings are folded along the back of the insect, the hindwings are not visible.

Remarks. The absence of reference by Cockerell to denticles on the mandible cannot be taken too seriously since such denticles, unless very prominently displayed on an open mandible, are not easy to see. Cockerell's specimen was listed with characters in 1908, but not fully described until 1909.

Genus *TRIGONA* Jurine 1807

*1807 *Trigona* Jurine : 246.
1896 *Meliponorytes* Tosi : 352 (type species *Meliponorytes succini* Tosi).

Genotype. *Apis amalthea* Olivier 1789, by subsequent designation of Latreille (1810 : 439).

Diagnosis. Stigma well developed, rounded below ; wings relatively long, extending beyond apex of abdomen ; hamuli about five or six, rarely more than nine or fewer than four ; body length from 2 to 8 mm, rarely exceeding 11 mm.

Remarks. The genus *Meliponorytes* was erected by Tosi (1896) to embrace forms ancestral to Recent Meliponini. All the fossils so far discovered and which have recognizable descriptions, however, are believed to be referable to *Trigona*. But the creation of the new genus *Meliponorytes* for what is apparently a genuine *Trigona* must have been a deliberate procedure, since Tosi makes mention of the likeness of his specimens to *Trigona* and also to the subgenus *Tetragona*. *Meliponorytes* was thus undoubtedly erected on account of those slight uncertainties attending fossil forms, although the action here seems scarcely justifiable. Tosi's descriptions and illustrations have been very carefully studied and there seems little doubt that his *M. succini* (see p. 221) is definitely a *Trigona* of the subgenus *Tetragona*, whilst the subgenus cannot be stated for his *M. sicula* (p. 224). Kerr & Maule (1964) thought that *M. succini* belonged to *Meliponula*, but in a different subgenus from *M. boccandei*.

---

[7] Not, as stated by Cockerell for his specimen, a considerable amount, though it is the most we have noticed among Baltic amber bees.

It will be recalled that all *Trigona* species lack hind tibial spurs, yet all, except *Lestrimelitta*, possess the hind tibial comb. The variations of the basitibial surfaces are of subgeneric value. [For subgenus *Nogueirapis* see Appendix, p. 257.]

Subgenus ***TRIGONA*** Jurine 1807

*1807 *Trigona* Jurine : 245.

GENOTYPE. *Apis amalthea* Olivier 1789.

DIAGNOSIS. (From Schwarz 1948.) Mandible toothed usually from end to end along its apex, or with three teeth on at least the outer two-thirds of the apex and an angulation at the inner extremity. Hind tibiae a little longer than the combined length of their femora and trochanters. The fringe along the posterior lateral contour of the hind tibiae with plumose hairs in addition to the usually sparser simple hairs. The base of the inner face of the hind basitarsi with a differentiated, more or less oval, area of appressed hairs that contrast with the brush-like hairs on the apical half to two-thirds of this inner face.

REMARKS. At least one fossil form is so far known, from the Pleistocene.

Trigona (Trigona) erythra Schletterer 1891

*1891 *Trigona erythra* Schletterer : 2.
1895 *Melipona togoensis* Stadelmann : 620.
1948 *Trigona erythra* var. *togoensis* Stadelmann ; Schwarz : 51, 61, 68, 132.
1961 *Axestotrigona erythra* (Schletterer) ; Moure : 239.
1961 *Axestotrigona togoensis* (Stadelmann) ; Moure : 239.

FOSSIL SPECIMEN STUDIED. British Museum (Natural History), In.17664.

DISTRIBUTION. Pleistocene : East African copal ; and Recent.

DESCRIPTION. Body length 5·75 mm ; general colour brownish-black to black. Head broader than thorax, hairs upright and relatively strong on vertex, ocelli prominent, in a gently curved line, hind ocelli more distant from each other than from compound eyes ; from the front ocellus there runs a prominent frontal line ; face, particularly the clypeus, appears to be covered with a close white pubescence ; length of scape little more than half the length of the flagellum, and all flagellar segments, except the last, not longer than broad, the last being longer than broad, and pointed.

Thorax markedly triangular, black, its surface matt, probably due to a short pubescence and to very fine rugosity ; longitudinal line through scutum (median mesoscutal line) masked by a crack in the amber, but the polished and shining furrow between scutum and scutellum can just be recognized ; scutellum clearly projecting, with strong chitinized hairs on its ridge.

Abdomen dark in colour with only few traces of brown, anterior segments smooth and shiny, hind segments covered with short pubescence ; legs on the whole black but not sufficiently well preserved at extremities to judge whether the latter are brown (most have been cut off short at the edge of the copal); corbicula well formed, wide, neatly hollowed, inner surface difficult to see; one basitarsus detached, the other wanting; claws not notched.

Marginal cell of forewing a little open at apex; one rather weak submarginal cross vein; first recurrent distinctly angular before junction with vein M; seven hamuli.

REMARKS. No diagnosis is given because the taxonomic position of the Recent species is still *sub judice*, and we are not sufficiently acquainted with previous investigations concerning this group to be able to make a useful contribution.

The fossil agrees with Recent specimens of *Trigona togoensis* Stadelmann in the British Museum (Natural History) and our description of the fossil agrees in all essential respects with the original description of *T. togoensis* by Stadelmann.

The two Recent forms *T. togoensis* and *T. erythra* differ in the colour of the abdomen, which is rusty red in the latter. *T. togoensis* is also slightly smaller. Schwarz, however, regards these differences at best as of varietal value, and we have followed him in regarding them as races of a single species. In the colour of the abdomen, the fossil from East Africa agrees with the West African form *T. togoensis*.

Subgenus ***Hypotrigona*** Cockerell 1934

*1934 *Hypotrigona* Cockerell: 54.
1961 *Liotrigona* Moure: 223 (type species *Trigona bottegoi* Magretti).
1961 *Hypotrigona* Moure: 220.

GENOTYPE. *Trigona gribodoi* Magretti 1884, by original designation.

DIAGNOSIS. Minute bees, with dull tegument but without true yellow marks. Clypeus flat, a little wider than twice its length and one-third as long as clypeocular distance. Lateral portion of epistomal suture straight. Mandible bidentate. Scape short. Flagellar segments very short. Bifurcation between M and Cu after cu-an. Submarginal angle about 90°. Hind basitarsus about twice as long as broad. [See also Appendix, p. 256.]

Trigona (Hypotrigona) gribodoi Magretti 1884

(Pl. 2, figs 5–7)

*1884 *Trigona gribodoi* Magretti: 630.
1894 *Trigona braunsi* Kohl: 280.
1895 *Trigona bottegoi* Magretti: 156.
1934 *Trigona* (*Hypotrigona*) *gribodoi* Magretti; Cockerell: 54.
1934 *Trigona* (*Hypotrigona*) *bottegoi* Magretti; Cockerell: 55.
1961 *Hypotrigona gribodoi* (Magretti); Moure: 220.
1961 *Liotrigona bottegoi* (Magretti); Moure: 223.
1964 *Trigona* (*Hypotrigona*) *gribodoi* Magretti; Kerr & Maule: 7.
1964 *Trigona* (*Liotrigona*) *bottegoi* (Magretti); Kerr & Maule: 7.

Specimens studied. British Museum (Natural History), In.38982–38993, In.17686, In.18209, In.18214, In.18220, In.18226, 58511, 58622.

Distribution. Recent (common in Africa); Late Pleistocene: East African copal.

Diagnosis. Length of body not exceeding 4 mm; head and thorax black, abdomen and eyes dark brown. There is no apparent natural testaceous coloration of the scape, mandibles or anterior legs. The body is only sparsely haired except, chiefly, for the ridge of the scutellum and the basitarsi; hind tibia triangular, neither clavate nor club-shaped, the inner face showing an elevated plateau-like area with a posterior rim.

Description. Face round, black; antennae of only moderate length, flagellum broad and shortish; ocelli prominent. Although the whole face appears uniformly black, the copal is believed to mask its short white pubescence, except in In.38993. The same is true of the hairs on the black thorax, but the stronger, more heavily chitinized hairs of the scutellum can be distinguished. Hind tibia not copiously haired, and because the hairs are fuscous they are sometimes difficult to see. All the tarsi appear to be more strongly haired than the tibiae. Wings hyaline; hamuli five or six, stigma well developed, marginal cell open at apex, no submarginal cross veins in evidence, except sometimes a stump for the first.

Some specimens show a very strongly reduced venation particularly of the posterior apical region of the forewing. The yellow rim to the compound eyes, so often noticeable in copal specimens, is believed to be due to the medium of their preservation.

Remarks. The following are brief statements on the insect inclusions of each numbered piece of copal preserved in the British Museum collection. The first twelve pieces come from the Luke Thomas Collection.

In.38982. One typical *T.* (*Hypotrigona*) *gribodoi*, and also a second inclusion of an insect believed to be a termite but whose head and thorax have been removed during the polishing of the copal.

In.38983. A well-preserved specimen of *T.* (*H.*) *gribodoi*, with quite a dark abdomen.

In.38984. Eight insect inclusions, i.e. six *T.* (*H.*) *gribodoi*, one dipteron and one termite. Some are most excellently preserved, and one of the bees shows an advanced reduction of the veins of the forewing.

In.38985. One *T.* (*H.*) *gribodoi* and various other chitinous remains of insects, including aculeates. The bee is poorly preserved, portions of it having been worn away during the polishing of the copal, but sufficient remains for it to be identified.

In.38986. Two *T.* (*H.*) *gribodoi*, both well preserved.

In.38987. Copal too cracked for accurate diagnosis, but contains one insect which appears to be a *T.* (*H.*) *gribodoi*.

In.38988. A poorly preserved specimen of *T.* (*H.*) *gribodoi*. Copal around the insect somewhat cracked. A second inclusion, again rather poorly preserved, but markedly petiolate, is believed to be an ant of the genus *Crematogaster*.

In.38989. A *T.* (*H.*) *gribodoi*, well preserved.

In.38990. A well-preserved *T.* (*H.*) *gribodoi*, and a second unidentifiable inclusion.

In.38991. Two *T.* (*H.*) *gribodoi*, one very well preserved, the other somewhat less so, on account of its position on the edge of the piece of copal, which is slightly cracked.

In.38992. One well-preserved *T.* (*H.*) *gribodoi.*

In.38993. Two *T.* (*H.*) *gribodoi*, one better preserved than the other. Here the pubescence, so characteristic of the species, is plainly visible. Both show a little coating of hair.

58511. All six insect inclusions appear to be *T.* (*H.*) *gribodoi.* In copal stated to be from Stettin on the Baltic, purchased from J. C. Rees 1867. There is, however, strong evidence from the so-called 'Baltic copal' from Stettin was imported from East Africa.

In.17686. Two *T.* (*H.*) *gribodoi.* Copal: East Africa.

The characters of the following specimens agree more with the original description of *T. bottegoi* Magretti than with *T.* (*H.*) *gribodoi* Magretti. Unfortunately, our study of Recent and fossil material leads us to believe that the characters selected by Magretti are not constant enough for the separation of the two species, and we have thus been compelled to sink the former species under the latter.[8]

In.18229. A well-preserved *T.* (*H.*) *gribodoi* with a detached head of the same species. The colour of the insect has been somewhat intensified by the copal and part of the ventral surface of the thorax, abdomen and legs appear whitish. This is probably because of air bubbles under the chitin of the insect.

In.18214. At first glance the insect in this piece of copal appears different from the other specimens mentioned above, owing particularly to the yellow-brown abdomen, ruby eyes and the reddish-tinted cloud on the apical region of the fore-wings. This intensified colour, however, appears to be some effect of the copal.

In.18220. Two *T.* (*H.*) *gribodoi*, and additionally two well-preserved detached legs almost certainly belonging to the same species. One of the two insects is well preserved but the upper portion of the head and thorax has been pared away during the polishing of the copal and it is surrounded by cracks. The second insect is also well preserved but again has a distinct reddish tinge, particularly noticeable in the eyes.

In.18226. A single *T.* (*H.*) *gribodoi*, fairly well preserved but with the head partly pared away. Thorax and legs show many white 'air-bubbles'. On the abdomen the pale bands indicate exposure of the thin intersegmental membrane as a result of distension of the abdomen.

58622. A single specimen surrounded by fairly copious air-bubbles in the copal. However, from the side, the specimen is relatively clear to view and is seen to belong to *T.* (*H.*) *gribodoi.* A white rim to the eye and the white sheen to the wings are believed to be spurious effects. It is slightly larger than the others, but the size of worker bees often varies considerably.

---

[8] The characters chosen by Magretti (1895 : 157) to separate *T. bottegoi* from *T. gribodoi* were: 'per la superfice minutissimamenta punteggiata, quasi liscia e nettamente splendente del capo, del mesonoto e dello scudetto; per presentare l'area dell'ocello mediano e la linea mediana frontale leggiermente distinte ed infine per la colorazione giallo-testacea dello scapo antennale, delle mandibole, del labro et delle due paia di zampe anteriori.' [. . . in having the surface very finely punctured, being almost smooth and distinctly shiny on head, mesonotum and scutellum; in showing the area of the median ocellus and the median frontal line faintly distinct and finally by the yellow-testaceous colour of the antennal scape, of the mandibles, labrum and the two anterior pairs of legs.]

Subgenus *TETRAGONA* Lepeletier & Serville 1828

*1828 *Tetragona* Lepeletier & Serville : 710.

Genotype. *Trigona elongata* Lepeletier & Serville 1828 (= *Centris clavipes* Fabricius 1804).

Diagnosis. The inner face of the hind tibiae unevenly gabled but with a sharply elevated, median, plateau-like area that extends from the base almost to the apex and contrasts strongly with a wide, flat, posterior rim (particularly widened at the apex) ; the contour of the hind tibiae more or less clavate, with the apex in all cases much wider than the base and sometimes conspicuously expanded ; plumose hairs in addition to simple hairs usually present along the posterior lateral contour of the hind tibiae or present over their outer face near the base, or both.

Remarks. The above is *verbatim* from Schwarz (1948).

Trigona (Tetragona) succini (Tosi 1896)

*1896 *Meliponorytes succini* Tosi : 352, pl. 6, figs 1–8.
1907 *Meliponorytes succini* Tosi ; Handlirsch : 892.
1909d *Meliponorytes succini* Tosi ; Cockerell : 5.
1925 *Meliponorytes succini* Tosi ; Schröder : 254.
1928 *Meliponorytes succini* Tosi ; Wheeler : 97.
1948 *Meliponorytes succini* Tosi ; Schwarz : 8.
1964 *Meliponorytes succini* Tosi ; Kerr & Maule : 2.

Holotype and Paratypes. Museo di Mineralogia dell'Univ. di Bologna.

Distribution. Miocene, Sicilian amber.

Diagnosis. Length 4 mm ; head subquadrangular, mandibles apparently with only two denticles ; inner surface of hind tibia plateau-like, of sharp elevation, with the posterior and apical rim fairly flat and wide ; inner face of hind basitarsus contains a smooth, bristleless area ; the hairs along the posterior edge of tibia appear to be plumose.

Description. Dark, except abdomen which tends to be reddish. Compound eyes large, oval and naked. Ocelli situated in a slightly curved line, the lateral ones prominent, the median one lying in a furrow. Face slightly convex, pubescent, and the facial area itself ellipsoidal, slightly hairy and prominent. Clypeus almost triangular and provided with hairs. Vertex double-humped, divided by a median sulcus. Antenna twelve-segmented, the scape long, about one-third the length of the antenna, creased at point of insertion. The structure of the antenna is given in some detail by Tosi, but cannot be said to differ materially from the Recent *Tetragona*, unless Tosi's implication of the rather naked first to third flagellar segments is regarded as significant. Labrum extended, 'becoming round and hollowed like a bowl'. Mandibles with two denticles. Tongue hairy with dilated apex. Labial palps apparently four-segmented with long first segment. Thorax essentially as in Recent *Tetragona*, with long hairs on ridge of scutellum. Tegulae well developed.

Wings hyaline but hairy, not extending much beyond the abdomen which appears to be fully extended (maybe distended). The main features of the forewing are as follows. Stigma very distinct, lanceolate in form ; first submarginal cross vein not strong ; marginal cell open at its extremity.

An antennal cleaner is present, and its 'auschnitt' lined with hairs. Basitarsus as long as the remaining tarsal joints taken together and covered with setae. Posterior tibia well developed and covered apically with thick, long hairs, but basally with fewer and more robust hairs. Last tarsal joint larger than the others (except the basitarsus) and cylindrical. Pulvillus large.

Abdomen ovoid, segments all the same size with longer hairs along posterior rim. First abdominal segment hollowed anteriorly. Ventral surface hulled and its first segment furnished with rows of longish hairs. A median sulcus follows the shape of the rows.

REMARKS. This species has been placed in the subgenus *Tetragona* not only on general morphology, but particularly on the structure of the hind leg. If Tosi's figures are carefully examined the inner surface of the hind tibia shows both a main ridge and also a clear dark zone posterior to it. This provides reasonable evidence that the inner surface is indeed plateau-like, of sharp elevation, with a flat posterior rim.

Schwarz (1948) who reviewed Tosi's species came to no definite conclusion with regard to them. He did, however, raise some meticulous points, and rightly or wrongly insisted upon very minute and difficult detail. He refers, for instance, to the two denticles on the outer half of the apex of the mandible instead of the inner half. It is true Tosi illustrated them in such a position and number, and this may have been accurate for a Miocene genus, but it must in any case have been an achievement for Tosi to recognize denticles at all. The distinction of inner and outer halves may have been well-nigh impossible. Again the appearance of obliqueness of the lateral ocelli is obviously influenced by the diffraction of light through the uneven amber surface and cannot be given the significance which Schwarz would like to attribute to it. The latter's reference to the length of the wing and to the stigma is non-committal.

Trigona (Tetragona) iridipennis Smith 1854

(Pl. 2, figs 8, 9)

*1854 *Trigona iridipennis* Smith : 413.
1858 *Trigona laeviceps* Smith : 51.
1921 *Meliponorytes* (?) *devictus* Cockerell ; Cockerell : 544, text-fig. 4.
1922 *Trigona laeviceps* Smith ; Cockerell : 714.
1922 *Meliponorytes* (?) *devictus* Cockerell ; Cockerell : 714.
1964 *Trigona* (*Tetragonula*) *devictus* Cockerell ; Kerr & Maule : 11.

SPECIMENS STUDIED. British Museum (Natural History), In.20702 (holotype of *Meliponorytes* (?) *devictus* Cockerell) and In.43809 (identified by Cockerell as *Trigona laeviceps* Smith).

Fossil distribution. Probably Pleistocene, Burmese amber : Hukong Valley.

Diagnosis. Length 4 mm. Head and thorax black, face with short, silvery pubescence rather variably distributed, labrum and mandibles ferruginous, antennae testaceous, margins of thorax and scutellum fringed with fuscous pubescence and the sides of the metathorax with a silvery pubescence, elsewhere smooth and shiny ; wings subhyaline, iridescent ; abdomen ferruginous or the base testaceous, smooth and shining, extreme apex pale testaceous, ventral surface with short, silvery pubescence ; apical joints of tarsi testaceous.

Description. Cockerell's description of specimen In.20702 apparently reflects the distortion which would be encountered in looking through the spherical bead containing the specimen, but the bead has now been cut and the following details may be regarded as reliable. Length 4 mm. Head and thorax black, the abdomen and mandibles ferruginous, tarsi testaceous. The naked eyes are red but this cannot be considered the natural colour, the head is broad but not unnaturally so, and the ocelli are prominent, in a curve on the vertex, and have also taken on the reddish tinge. The antennae appear normal in position, size and shape for *T.* (*T.*) *iridipennis* ; the scape certainly cannot be considered long and the curve is only slight ; the flagellum is thick and short.

The mesothorax is raised and the scutellum projects, but neither of these features is striking. Hairs are not much in evidence but a few can be perceived on the thorax and on the ridge of the scutellum ; this apparent nakedness, however, is what must be expected of white pubescence on fossilization in amber.

Femora not especially robust, hind tibiae broadened at apex, triangular rather than clavate. Hind basitarsi are at most only half the length of the tibiae and cannot be described as large ; on the other hand, the abdomen is not short for the size of the creature. Forewings subhyaline with a well-developed pale stigma, but folded over the body so that the venation cannot be determined, except that the junction of the basal nerve and cross vein cu-a is coincident. Claws simple, pulvilli large.

The specimen In.43809 was referred by Cockerell to the Recent *Trigona laeviceps* Smith, which is synonymous with *T.* (*Tetragona*) *iridipennis* Smith.

Remarks. Although the specimens look different, when examined superficially, the abdomen of '*M. devictus*' being long and that of '*T. laeviceps*' short, broad and curved downwards, they are conspecific since the differences in the abdomen are due to accidents of fossilization, the first being inflated by gases of putrefaction, the other strongly constricted, as if dried.

'*T. laeviceps*' Smith had already been synonymized with *T. iridipennis* Smith by Schwarz (1948). On the other hand, the comparison of *M. devictus* with Recent species has led us to its identification with *T.* (*T.*) *iridipennis*. Cockerell, therefore, was mistaken in assigning these two specimens to two different genera and species.

The reasons for Cockerell's mistake are interesting. In 1921 when Cockerell investigated the first piece of amber, he was under the impression that it was of Miocene age and in consequence placed his specimen under a Miocene genus, *Meliponorytes*. It was in the following year that he received a communication to the effect that this amber was, in fact, very much more recent. Consequently the specimen described in that year was referred to the modern *Trigona laeviceps* Smith which, as we have seen above, is a synonym of *T.* (*Tetragona*) *iridipennis* Smith. Unfortunately Cockerell never rechecked the specimen he designated as *Meliponorytes* (?) *devictus* and in consequence the latter name has persisted in the literature until now.

Subgenus indet.

Trigona sicula (Tosi 1896)

*1896 *Meliponorytes sicula* Tosi : 355, fig. 9.
1928 *Meliponorytes sicula* Tosi ; Wheeler : 97.
1948 *Meliponorytes sicula* Tosi ; Schwarz : 9.

Holotype and Paratypes. Museo di Mineralogia dell'Univ. di Bologna.

Distribution. Miocene : Sicilian amber.

Diagnosis. Three times larger than *T.* (*Tetragona*) *succini*, i.e. about 12 mm long ; mesonotum a little less arc-shaped, hind basitarsus narrower and longer. Mandibles with two terminal notches ; pterostigma wanting.

Description. The following characters are common with those of *T.* (*Tetragona*) *succini* : (1) large oval eyes, (2) situation of ocelli, (3) antennae, (4) labial palps, (5) claws and pulvillus, (6) hairy tongue, (7) prominent scutellem with long hair. The species appears to have been rather dark in coloration and the wing very similar to that of *T.* (*T.*) *succini* except for the lack of stigma.

Remarks. The subgenus unfortunately cannot be determined. The specimens themselves are sufficiently like *succini* to be considered to belong to *Trigona*, although they lack the stigma, but their large size is a little perplexing. Again, the specimens are not well preserved, and in consequence inadequately described. Tosi wondered whether the species was not a *Melipona*, but in view of the present limited distribution of the latter in South America, and the prevalent ideas of the phylogeny of this group, the latter suggestion is not a happy one. Only a re-examination of the type may shed light on the problem. The diagnosis given above is of necessity comparative, in view of Tosi's manner of description. Yet it must be remembered that the stigma illustrated by Tosi is much as in some *Tetragona*. Again, the comb and pollen rake of the hind tibia are notoriously difficult to detect in some fossil forms and are poorly developed in some Recent members of *Tetragona*. Failure to detect them, therefore, may be taken as an indication of their smallness, not of their absence.

The decision to include the present specimens in *Tetragona* was mainly the result of a study of their leg contours, as already mentioned. The wing venation, however, caused difficulty. According to Tosi vein Cu_2 is redundant and vein Cu_1 meets vein A at the distal and lower apex of cell 2nd Cu. Nevertheless, a slight furrow, which appears to exist in this vicinity in Recent forms, could, if it existed in fossil forms, have given rise to the latter illusion. Again, since the junction of the veins

Cu_1, A and Cu is unknown in Apidae, it is fairly obvious that a mistake has been made here. With regard to cross vein cu-a, not only does it lie along a rather abnormal slope but its relation to the basal vein is peculiar. Possibly in his figure Tosi has rather unwittingly exaggerated the junctions of the veins in this region in an effort to clarify their course.

More than eight specimens of these fossil bees were found in one piece of amber.

Tribe **APINI** Latreille 1802

DESCRIPTION. This Old World tribe is unique among bees in the form of the male genitalia which, unfortunately, are as a rule not accessible in fossil forms.

The Apini have the following characters in common with the Meliponini : scutellum raised, malar space short, ninth sternum modified. Forewing with first recurrent vein angulate or curved. Hindwing with jugal and anal lobes.

The following features are diagnostic for Apini. Eyes densely hairy in Recent forms. Sting well developed. Either one outer tibial spur on hind leg or none ; hind basitarsus usually broad as tibia and always rectangular, with a depstum, or the latter broadened into an auricle ; basitarsal brush without the small bristleless or differentiated area ; claws cleft.

Wings never extending much beyond the body. Distal cells of forewing always complete, marginal cell parallel-sided for a large part of its length in Recent species, but not parallel-sided and smaller and deeper in early fossil forms ; pterostigma becoming reduced, not tapering beyond base of vein r.

REMARKS. Most of the known fossil Apidae belong to this tribe, the most important and interesting of all as it embraces the honey bee *Apis mellifera* (p. 249). As a result, the evolution of this remarkable insect can be reconstructed in a detailed manner.

Genus ***ELECTRAPIS*** Cockerell 1908

*1908b *Electrapis* Cockerell : 326.
1909d *Electrapis* Cockerell ; Cockerell : 7.

GENOTYPE. *Apis meliponoides* Buttel-Reepen 1906, by monotypy (Cockerell 1908).

DIAGNOSIS. Body morphology not very bomboid (p. 157) but wing venation retaining bomboid characters. Either a single outer hind tibial spur or none. While the body may have a variable quantity of hair, that on the eyes is scant or non-existent.

DESCRIPTION. Variable in size and shape ; from 4 mm to 14 mm in length. Normal disposition of tip of abdomen slightly ventral and proximal.

Head. Moderately large and somewhat square ; tuft of hair on the vertex often present ; compound eyes moderately convex and ocelli prominent. Male has eyes far apart and the facial quadrangle is squarish.

Mouth parts are well known only from Cockerell's descriptions, which may not apply to all species. They are as follows. 'Mandibles truncate, much as in *Apis*, but the cutting edge with two notches ; labrum semicircular, tongue elongate and both it and the labial palpi essentially as in *Apis* ; spoon on end of tongue small, maxillary palpi very small, thick, apparently 2-jointed, malar space very short ; anterior end of clypeus straight'. The little that can be discerned in *E. apoides* Manning, however, suggests a single notch in the cutting edge of the mandibles, and an elongate 'tongue' with a rather large flabellum.

Antennae moderately long, sockets large ; scape relatively long and curved, usually broadened distally and often articulating with a 'knob-shaped' pedicel or first joint of the flagellum. Male antennae longer than female.

Thorax variable ; (1) long and broad in proportion to the size of the insect, tapering sharply distally, very reminiscent of some *Trigona* ; (2) less broad and more slender, proportionately more reminiscent of *Apis* ; (3) more spherical in shape, usually well covered with hair, somewhat reminiscent of *Bombus*. Scutellum always distinct and often prominent.

Front leg. Antenna cleaner always present but structurally slightly different from Recent *Apis*.

Middle leg. Outer surface of tibia well provided with stout hairs. A single spur present at apex of tibia, stouter than that of hind leg. Basitarsus with long strong hairs.

Hind leg. Tibia much longer than basitarsus. Posterior fringe of hairs on the tibia well developed and believed to contain some plumose hairs among the simple ones. Corbicula and pollen rake present. Sometimes a ridge covered with fine hairs occurs on the inner surface of the tibia. Basitarsus rectangular, with a brush and often a small differentiated area.

Claws bifid. **Pulvilli** fairly large.

Abdomen. Usually oval in shape and, at most, only moderately clothed with hair. In *E.* (*Roussyana*) *palmnickenensis* the hairiness of the sternites resembles an abdominal brush, usually as broad as the tibia or nearly so. The shape of the abdomen as figured by Buttel-Reepen (1906) may not be typical of the whole genus ; another known type has one edge convex, more like that of a recent *Apis* worker. The 'auschnitt' of the auricle between tibia and tarsus is deep and well formed, but there is only an incipient development of the depstum. A single outer spur is typically present.

Forewing. Pterostigma variable in size and shape. Marginal cell moderately long and generally broader than that of Recent *Apis*, ending away from wing margin in a stub. Vein second r-m always curved, mostly S-shaped, but much more upright than in Recent *Apis* and meeting M very slightly distad of the junction of M and second m-cu ; first r-m at right angles to M ; base veins of cells first R_1 and first Rs form a Y with first submarginal cross vein ; the junction of first m-cu with M is angular as described, but not illustrated, by Cockerell (1909d). This junction is beyond half the wing length and thus much more distal than in Recent *Apis*.

The basal vein meets at the base or just proximad of stigma and is gently S-shaped. It runs into Cu slightly proximad of the junction of the latter with cross vein cu-a, or the junctions here coincide. Lower section of basal vein (M) not less than twice the length of the upper section of basal vein (Rs). Vein Cu_2 is fairly short.

Hindwing. Hamuli variable (6–16, cf. *Chalcobombus* with 8–11). Cross vein cu-a oblique, the slope being posterior and basad, as in Recent *Bombus* and opposite in direction to that of Recent *Apis* ; M runs almost to wing margin ; cross vein r-m well defined, but only at most, slightly oblique, while Rs, like M, almost reaches wing margin. The general shape is more elongate than Recent *Apis*, and the wing possesses distinct and well-characterized anal and jugal lobes.

Wings, in general, hyaline, fuliginous or fuscous and of moderate size, rarely longer than the body length though from their point of insertion on the thorax they often extend beyond the abdomen. Sometimes a fairly large, dark-coloured cloud (about one-twelfth total area) is present in the forewing. Most wings are hairy, but there is some doubt as to whether this applies to all species.

Remarks. Most authors have held *Electrapis* to be directly ancestral to Recent *Apis*. This view is likely to be correct regarding only *Electrapis* s. str., here treated as a subgenus. The other species show clear signs of deviation. On the whole, however, one cannot separate these groups as distinct genera, as too many characters overlap. It is in fact impossible to give clear diagnoses of subgenera, and the three subgenera here distinguished are to that extent arbitrary. They are :

(1) a group with *Apis*-like characters : *Electrapis* Cockerell 1909d, s. str. ;
(2) a group with *Bombus*-like body and *Apis*-like venation ; *Protobombus* Cockerell 1908b ;
(3) a *Trigona*-like group : *Roussyana* Manning 1960.

Cockerell (1909d) and Zeuner (1944, 1951) considered that the species of *Electrapis* were social insects. As evidence Cockerell pointed out the occurrence of many specimens crowded together in a small piece of amber (*E. meliponoides*), whilst Zeuner considered the structure of the collecting apparatus. On other grounds too, this contention can be supported. [See also Appendix, p. 257.]

Subgenus *ELECTRAPIS* Cockerell 1908

*1908b *Electrapis* Cockerell : 326.
1909d *Electrapis* Cockerell ; Cockerell : 7.

Genotype. *Apis meliponoides* Buttel-Reepen 1906, by monotypy (Cockerell 1908b).

Electrapis (Electrapis) apoides Manning 1960

*1960 *Electrapis* (*Electrapis*) *apoides* Manning : 306, pl. 5, fig. 1.
1970a *Electrapis apoides* Manning ; Kelner-Pillault : 16, pl. 2, figs 1, 2, text-fig. 5A.

Holotype. No. 94 in the Bursey Collection (see p. 159), now in the Muséum National d'Histoire Naturelle, Paris.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Body 6·5 mm long, hairy. Forewing 6 mm. Hind tibia comparatively short and stout, with a single, much reduced, spur ; corbicula exceptionally well developed with strong curved hairs on the posterior edge ; basitarsus square and flat, but with the posterior edge markedly convex. Wings fuliginous with a cloud apically ; pterostigma large ; eight hamuli.

DESCRIPTION. Specimen well preserved, blackish. Total length 6·5 mm ; thorax 2·75 mm long and 2·25 mm wide ; abdomen 2·75 mm long and 2·5 mm wide ; forewing 6 mm ; hind tibia 2·75 mm.

Proboscis extended for approximately the length of the head, provided with a large flagellum. Antennae very much like those of *E.* (*Roussyana*) *proava* (p. 236), with a similarly shaped, knob-like pedicel.

The forelegs differ from those of other species of *Electrapis* in the shape of the antenna-cleaner. The zone of articulation between tibia and tarsus is greatly reduced, and the latter limbs are rounded, and not square, at their point of insertion. The clasp, too, is more highly developed, now having a fully shaped lobe and a distal tip projecting over and against the distal edge of the notch. The middle legs cannot be studied in detail, since they lie too much under the body of the insect. They are, however, well provided with hairs and appear to possess a single strong spur.

The hind legs are well proportioned, and not lanky as in *E.* (*Roussyana*) *proava*, and the hairs of the posterior margin of the corbicula are possibly plumose. On the apical margin of the tibia, posteriorly, a fine-haired rake is present, and the 'auschnitt' of the auricle is well developed. Moreover, the internal spur on the hind tibia is present and visible on the left leg of the specimen as viewed from behind. It is thicker and about one and a half times as long as the hairs of the anterior edge of the leg, but it is evidently in a state of reduction, being so small as hardly to serve any useful purpose. The basitarsus, although squarish, is elegantly shaped, with graceful curved outline, and not coarsely square as illustrated by Cockerell for *Chalcobombus*. Its inner surface is equipped with strong, almost bristle-like, hairs, which are arranged in rows as can be seen for those situated at the distal extremity.

The wing venation does not differ materially from that of *E.* (*R.*) *proava*. Possibly the basal nerve of the forewing is slightly less curved, and the radius stronger. The hindwing is preserved in its entirety and exhibits eight hamuli, and well-developed jugal and anal lobes. Only one anal vein is known to be present, but the two lobes are separated by a deep cleft. A line that could be regarded as 4H is probably no more than a fault in the amber. Veins Rs and M continue almost to the wing margin, cross vein r-m slopes basad posteriorly, and cross vein cu-a exhibits a similar, but more oblique, slope.

On the whole, the creature itself has the habitus of a small *Apis*. The head is well proportioned and neatly tapering, less square than some other species of *Electrapis*, and the thorax has neither excessive width nor length. The abdomen, however, is still rather small, though the habit of holding the tip ventrally, together with the presence of an air bubble on this particular specimen, rather prevents accurate observation of this point. The wings still project some distance beyond the apex of the abdomen.

REMARKS. The specimen was kindly lent by the late Mr Bursey of Surbiton, Surrey, to whom we acknowledge our thanks.

Electrapis (Electrapis) meliponoides (Buttel-Reepen 1906)

(Pl. 3, figs 5, 6)

*1906 *Apis meliponoides* Buttel-Reepen : 158.
1907 *Apis meliponoides* Buttel-Reepen ; Handlirsch : 892.
1908b *Electrapis meliponoides* (Buttel-Reepen) ; Cockerell : 326.
1909d *Electrapis meliponoides* (Buttel-Reepen) ; Cockerell : fig. 4.
1915 *Apis meliponoides* Buttel-Reepen ; Buttel-Reepen : 10, fig. 3.
1915 *Electrapis meliponoides* Butt.-Reep. ; Buttel-Reepen : 12.
1928 *Apis meliponoides* Buttel-Reepen ; Wheeler : 98.
1928 *Electrapis meliponoides* (Buttel-Reepen) ; Wheeler : 98.
1931 *Apis meliponoides* Buttel-Reepen ; Statz : 40.
1931 *Electrapis meliponoides* Butt.-Reep. ; Statz : 41, figs 2, 3.

HOLOTYPE AND PARATYPE. Two specimens in the Westpreussisches Provinzial-Museum, Danzig.

MATERIAL. Cockerell's specimens (1 male, 7 females), Koenigsberg Collection. Also Nos. 238 and 461 in Scheele Collection, Geologisches Staatsinstitut, Hamburg. No. 238 is also Typen-Katalog des Geol. Staatsinstitut, No. 149.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Body 14 mm. Body hairy but scant hair on eyes ; basitarsus comparatively long, broad and flat, posterior edge not convex ; wings fuliginous.

DESCRIPTION. Cockerell's description can be summarized as follows (the measurements quoted in hundredths of a millimetre by Cockerell are to a degree of precision as unnecessary as it is misleading). Black, much erect fuscous hair on head and thorax. Tibia and tarsus with coarse fuliginous hair ; wing venation remarkable only for the small, piceous, stigma ; it is thought, too, that the upper section of the basal vein is comparatively short. Male specimen with eyes far apart ; facial quadrangle square ; antennae long, over 5 mm with last joint obliquely truncate.

The following description is based on specimen No. 238 (Scheele Collection), which one of us (F. J. M.) was able to study in Hamburg. At first sight the fossil appears to be poorly preserved, in fact so much is covered with 'schimmel' that only a few segments of the abdomen can be discerned. The left forewing and hindwing, however, are both completely intact and the right forewing also shows much of the venation. Moreover, many parts of the legs are preserved, as well as the sting, and the hairiness of the thorax and the colour of the abdomen are clearly perceptible. Unfortunately, the head is completely missing.

The specimen has the following measurements : overall length, without head, 12 mm ; length of forewing, 9·5 mm ; hindwing 6 mm ; basitarsus 2·25 mm.

The copious hairs on the thorax are erect and fuscous. The abdomen is black, but each segment appears to have a band of dark brown distally ; it is hairy but the hairs are smaller and darker than those on the thorax. They are, however, longer at the apex of the abdomen. The sting protrudes considerably and is strong and straight. In Recent *Apis* a straight sting is characteristic of the worker, that of the queen being distinctly curved.

The many fragments of legs cannot be entirely pieced together. It is evident, however, that the claws are bifid and the distitarsi cordiform. The tibia, which can easily be recognized as such, has unfortunately had the outer surface pared away during the polishing of the amber. The corbicula, therefore, is lost, but the strong hairs of the anterior edge, which have not been destroyed, give complete proof of its earlier presence, if such were needed. There is no evidence for a tibial spur. This does not imply absence in view of the fragmentary character of the legs. The basitarsus is large, broad and flat, three-quarters the length of the tibia, the posterior edge quite straight and the posterior distal angle quite acute. Unfortunately the details of the structure at the junction of the basitarsus with the tibia are mostly masked by decayed pollen so that the depstum is not known. The strong non-plumose hairs of the anterior apex of the tibia, however, are present exactly as in Recent *Apis* and there is reason to suspect that the pollen rake has strong teeth. There is no evidence whatever for the presence of a pollen comb, but the pollen brush of the basitarsus is present. The strong hairs are arranged in rows with pollen still adhering to them. Approximately 17 hairs comprise the bottom row.

The hairy forewing has a large cloud, and is slightly papillate apically. The wing venation is that of *Electrapis* but a slight elongation of the wing itself has brought about a few minor modifications. These are a narrowing of the apex of the marginal cell, an elongation of the third submarginal cell and the second M. Proximally there is an increase in the length of the basal nerve with a consequent compensating alteration on the shapes of the first submarginal cell and the first M. The junction of basal nerve and cross vein cu-a is coincident on Cu, and vein cu-a slopes slightly apicad. Pterostigma piceous, but not small, though rather weak.

The hindwing is particularly interesting because of the increase of the number of hamuli to 16.

The other specimen from the Scheele Collection (No. 461) is poorly preserved, and covered with much 'schimmel'. Only part of a hindwing is well preserved. The insect is reminiscent of specimen No. 238, agreeing with it in all available characters. Length, with head, at least 13 mm ; hind basitarsus rectangular and long, almost as broad as tibia, and with a straight posterior edge ; hindwing in venation and shape agreeing with No. 238 except that the base is slightly shorter and the lobes deeper, and cross vein r-m appears more oblique. These characters can be accounted for by the oblique angle at which the wing must be viewed through the amber. At least 16 hamuli are present.

The remaining features are taxonomically unimportant. They include the presence of two well-developed antennae inserted on the lower half of the face ; thorax possibly well supplied with hairs ; wings extending to tip of abdomen and probably beyond ; and the presence of legs whose broad outlines only can be ascertained.

Remarks. Cockerell defined the hind basitarsus of his specimens as 'broad and flat, as figured by Buttel-Reepen (*Apis meliponoides*)'. His specimens are thus considered to be identifiable with the latter.

Buttel-Reepen was rather obsessed with the idea that *E. meliponoides* was intermediate in character between Recent stingless bees and Recent honey bees. What is probably true is that both groups evolved from some common ancestral form and that the Eocene *E. meliponoides* represents one member of this evolving series. Moreover, Buttel-Reepen stressed his point exclusively with regard to the hind basitarsus, which alone he described. From the descriptions here given, however, it is clear that the basitarsus has little that can be described as typically meliponid.

Electrapis (Electrapis) tornquisti Cockerell 1908

*1908b *Electrapis* (?) *tornquisti* Cocker*ell* : 326.
1909f *Electrapis* (?) *tornquisti* Cockerell ; Cockerell : 23.
1928 *Electrapis tornquisti* Cockerell ; Wheeler : 98.
1931 *Electrapis* (?) *tornquisti* Cockerell ; Statz : 41.
1931 *Electrapis tornquisti* Cockerell ; Salt : 145.

Holotype. Geological Museum, University of Koenigsberg.

Distribution. Eocene, Baltic amber.

Diagnosis. Length of body 11·5–12 mm ; robust and more *Bombus*-like than the previous species ; head and thorax abundantly hairy, but face with scant hair ; fourth antennal joint conspicuously shorter than fifth ; wing hyaline, stigma almost lacking ; hindwings with 15 hamuli ; abdomen broad.

Description. A hairy bee, more so than *E.* (*E.*) *meliponoides*. Coloration of thorax anomalous. The broad abdomen, although apparently black, has the hind margins of the segments rather broadly seamed with white. Pubescence of abdomen short and pale. Tegulae large with very fine delicately plumose hairs.

Venation differing from *E.* (*E.*) *meliponoides* in the rather distal position of the cross vein cu-a which lies slightly distad of the junction of the basal vein with Cu. It further differs in the lower part of this vein being strongly bent basad. It agrees with it, however, in that section Rs of the marginal cell is concave.

Remarks. Although this specimen, on general morphology, is more bomboid than other *Electrapis* s. str., it has been retained in this section for convenience. The species was listed with some characters in 1908, but was not fully described until 1909.

Subgenus ***PROTOBOMBUS*** Cockerell 1908

*1908b *Protobombus* Cockerell : 327.
1909d *Protobombus* Cockerell ; Cockerell : 10.

Genotype. *Protobombus indecisus* Cockerell 1908, by monotypy.

Diagnosis. Wings comparatively apoid, and more bomboid, than in *E.* (*Electrapis*).

DESCRIPTION. Body globose, compact and *Bombus*-like. Compared with *E.* (*Electrapis*) it appears to have a greater range of notches on the mandibles (1–3), the elevation of the scutellum is accentuated and the inner tooth of the claws is shallower. It agrees with *E.* (*Electrapis*) in size (7–10 mm), in its hairless eyes, comparatively large wings, gently convex posterior margin of the basitarsus, tibial spur of the middle leg, large ocelli and large pulvillus. The hind tibial spur may or may not be present.

Forewing. Stigma almost wanting. Marginal cell longer than in *E.* (*Electrapis*) but still ending obtusely at a distance from wing margin. All the submarginal cells exhibit peculiarities, in particular the second which is, according to Cockerell, 'very broad, pentagonal, much longer than third on marginal, and receiving 1st recurrent nervure (1st m-cu) at or a little beyond end of its first third'. The latter feature is remarkable in that it shows a definite advance towards the *Synapis* wing. This point, however, is further emphasized by the first and second submarginal cross veins being 'equally oblique in opposite directions', and also by the fact that the third submarginal cell is produced apically, by implication presumably more so than in the *E.* (*Electrapis*) wing. In these points the wing is markedly apoid. It is not a *Synapis* wing, however, since the base of the third submarginal cell receives the second m-cu vein one-sixth from its end, and the first m-cu has a bend or angle in its upper part. Such characteristics are typical of the genus *Electrapis* as are also the remaining characters quoted by Cockerell.

Hindwing. Vein cu-a strongly oblique with sometimes a slight double curve.

REMARKS. Cockerell considered this genus to be ancestral to *Bombus*. This point of view, however, is difficult to maintain since *Protobombus* has a more apoid wing than even *E.* (*Electrapis*), though its body is somewhat reminiscent of *Bombus*. The wide divergence from *Bombus* may be more easily appreciated if the evolutionary sequence of the second submarginal cell, in relation to the position at which it receives the first m-cu vein, is summarized:

Chalcobombus – beyond (distal of) the middle.
Electrapis (*Electrapis*) – just beyond or at the middle.
Electrapis (*Protobombus*) – much [Cockerell's term] before the middle.
Synapis – about one-third before middle.
Apis – about one-quarter before middle.

Electrapis (Protobombus) indecisus (Cockerell 1908)

*1908b *Protobombus indecisus* Cockerell : 326.
1909d *Protobombus indecisus* Cockerell ; Cockerell : 10, fig. 5.
1931 *Protobombus indecisus* Cockerell ; Salt : 146.

HOLOTYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. About 10 mm long ; mandibles obliquely truncate with three notches on cutting edge ; basitarsus broad.

Description. A blackish bee, but base of abdomen brownish, with sparse pale hair. Thorax and occiput densely covered with rather short, plumose, whitish hair. Legs and tegulae on the whole blackish with pale hair. The distinctive feature of the pale fuliginous wing is a dark cloud at end of marginal cell.

Remarks. Listed by Cockerell with a few characters in 1908, but not fully described until 1909.

Electrapis (Protobombus) tristellus (Cockerell 1909)

*1909f *Protobombus tristellus* Cockerell : 24.
1931 *Protobombus tristellus* Cockerell ; Salt : 146.

Holotype. Geological Museum, University of Koenigsberg.

Distribution. Eocene, Baltic amber.

Diagnosis. About 7 mm long ; much erect hair on vertex ; wings approximately 6·7 mm long ; abdominal segments black with hind margins 'rather broadly pale reddish' ; anterior margin of basitarsus gently convex ; glossa, as preserved, short ; mandibles long, falciform with a single deep notch ; last two joints of labial palpi rather large ; eyes wide apart above.

Description. A blackish bee ; mesothorax and scutellum as well as vertex with much erect black hair, abdomen as described above. The forewing has a large, conspicuous fuliginous cloud. Venation as in *E.* (*Protobombus*) *indecisus*, except for a presumed double curve of the long, oblique vein cu-a of hindwing. Mouth parts appear to be well preserved and differ in several respects from those of *E.* (*Electrapis*) *meliponoides*, for instance in the short broad glossa and the large flabellum. The length of the mouth parts, however, is difficult to ascertain in fossil forms, since they may not be completely extruded. Little reliance, therefore, should be placed on this character for diagnostic purposes.

Remarks. This specimen was not listed by Cockerell in 1908.

Subgenus ***ROUSSYANA*** Manning 1960

Genotype. *Apis palmnickenensis* Roussy 1927, by original designation.

Diagnosis. This subgenus embraces the more *Trigona*-like members of the genus *Electrapis*. These bees exhibit, however, all the characters of this genus, in so far as they are known. They are distinguished by the habitus of the body which is reminiscent of the stingless bees.

Electrapis (Roussyana) palmnickenensis (Roussy 1937)

(Pl. 3, figs 1, 2)

*1937 *Apis palmnickenensis* Roussy : 66, fig. 13.
1938 *Apis palmnickenensis* Roussy ; Armbruster : 89.
1960 *Electrapis* (*Roussyana*) *palmnickenensis* (Roussy) ; Manning : 306.

Holotype and Paratypes. Roussy Collection, Aigle, Switzerland.

Material. In addition to the types, one specimen in Geologisches Staatsinstitut Hamburg (Scheele Collection, No. 218; also listed in Typen-Katalog des Geol. Staatsinstitut, No. 150).

Distribution. Eocene, Baltic amber.

Diagnosis. Small, black insects about 4 mm long; scutellum very hairy; sternites with rows of hairs. Inner surface of tibia with a ridge of short hairs covering about a quarter of the posterior surface. Basitarsus less than half the length of, and narrower than, the tibia, its posterior upper apex exhibiting an area clear of bristles and an incipient depstum.

Description. We have inspected M. Roussy's piece of amber containing eight specimens, two of which are complete. The following is the condition of the individual specimens, their numbers agreeing with the semicircular alignment from the left upper corner of the piece of amber towards the right lower corner.

1. Badly preserved, except fore and hind legs. Wing venation masked by 'schimmel'. Possibly not more than 3·5 mm long.

2 and 3. Very much alike and well preserved; 3–4 mm long. Details of almost all appendages can be discerned including mandible and proboscis of No. 3. Spur on hind legs distinct. Wings of No. 2 not clear.

4. The best preserved specimen, but parts of some legs cut off. A considerable amount of wing venation can be discerned. 3·5 mm long.
5. Much covered by 'schimmel' but much of the wing venation recognizable. Antennae prominent.
6. Badly preserved and consists only of remains of thorax and legs.
7. Somewhat covered with 'schimmel' and wings cut off short. Insect bent on itself. One antenna present and well preserved.
8. Remains of a head with mandible.

The wings extend well beyond the apex of the abdomen; the head is broad, but less so than the thorax. The antennae are inserted on the lower part of the face and consist of a comparatively long, slightly curved scape and 11 segments to the flagellum; the pedicel appears to be knob-shaped. The eyes are prominent on the side of the head, and the ocelli distinct. The thorax is strong and carries a prominent scutellum. The abdomen is short and oval. The forelegs exhibit a well-developed antenna cleaner with broad flap and deeply rounded 'auschnitt', whilst the hind leg is characterized by a distinct corbicula with scopa, strong pollen rake, and short outer tibial spur but no pollen comb. The basitarsus is rectangular and equipped with a hairy pollen brush on the inside.

In addition to the eight specimens of M. Roussy, another has been found. It is preserved in the Scheele Collection, Hamburg. Through the kindness of Professor E. Voigt and Dr Walter Häntzschel it was lent to us for detailed inspection. Since the piece of amber contains one complete insect, perfectly preserved, and two fragments of legs, one in excellent condition showing tibia and tarsi, it has been possible to obtain a reasonably complete description of it, and the following is based on this specimen.

Size. From head to tip of wing 4·25 mm. Length of forewing 3·25 mm, extending 1·25 mm beyond the tip of the abdomen. Length of hind tibia and tarsus 2 mm. This specimen appears to be longer than the Roussy specimens, but this is deceptive. Though the wings extend conspicuously beyond the abdomen, the length of the body (which cannot be measured accurately) is possibly no more than 3 mm.

Colour. Very dark brown, or blackish. A creamy shading on the notum may be due to the natural colour of its copious hairs, or else it is due to the presence of some pollen.

Head moderately large, black, face sparsely hairy, with cream-coloured pubescence on the vertex. There is a reddish patch around the right ocellus, but this is almost certainly the result of *post mortem* alteration.

The compound eyes are hairless and prominent, and almost reach the bases of the mandibles, so that the malar spaces are much reduced. The three ocelli are large, set on the vertex and arranged in a shallow triangle. The single median frontal suture runs from the middle ocellus downwards.

The clypeus is trapezoid, tapering dorsally because of the convergent slope of the lateral epistomal sutures, and it is not protruding. The mandibles appear to have at least a convex cutting edge. The anterior part of the face terminates in a narrow labrum.

The antennae are not more than moderately long, inserted close together immediately above the frontoclypeal suture and apparently yellow and black. The scape has slightly less than half the length of the flagellum. The flagellum consists of eleven segments mostly subequal in size, though the terminal segment is longer, and those near the pedicel thinner and more tapering, and also darker in colour.

Thorax. Well developed ; pronotum short ; scutellum very prominent. The whole thorax copiously covered with hairs which are longest on the scutellum, but shorter on the pronotum. Tegulae large.

Abdomen. Small, oval. Tergites not noticeably hairy, though the sternites have rows of well-defined hairs. No intersegmental membranes can be discerned and this is taken as evidence of the rather contracted nature of the abdomen.

Wings. Hairy and fuscous ; pattern of wing venation as in *Electrapis*, with the following points of interest ; in the forewing the pterostigma is large and deep ; the anterior vein bounding the marginal cell, i.e. radius, is not coincident with the wing margin and its course continues beyond the apex of the marginal cell towards the wing apex ; cross vein cu-a lies distad of junction of basal nerve with Cu ; the hindwing has only six hamuli and both jugal and anal lobes are well developed.

Three anal veins are present in the hindwing. They can be seen if the left hindwing is viewed head-on, i.e. as inspecting the face of the insect.

Legs. Antenna cleaner present on foreleg, 'auschnitt' large, but since the legs are flexed on themselves other structures cannot be clearly identified ; middle leg has tibia at least as long as femur, broadening towards apex, and covered with strong hairs, particularly posteriorly. Pollen is entrapped in these hairs. A distinct tibial spur can be recognized on this leg.

The hind leg appears to have a comparatively large trochanter distinctly tapering towards the base ; tibia longer than femur, triangular in shape, and with a well-developed scopa ; hairs appear somewhat plumose ; corbicula moderately well developed, smooth, with few hairs within the corbicula itself ; inner surface of tibia with the ridge of short hairs occupying such a position posteriorly that the rim which separates it from the posterior edge of the corbicula is very narrow but the anterior rim is wide. The tibial appendages consist of a small, outer tibial spur, straight, and non-serrate, and a strong pollen rake projecting on a shelf from the inner apex of the tibia ; no pollen comb is present, but at the posterior apex of the tibia an angle suggests an incipient auricle. The tibia is not strongly curved, even posteriorly, but the isolated hind leg, because of the curve of the amber, deceptively gives this impression.

The basitarsus is narrower than the tibia and rectangular. The two posterior apices are strongly acute ; the inner surface consists of a brush of strong hairs, whose disposition in rows is rather masked by the comparatively great length of the bristles ; possibly five rows is the maximum, though the bristles per row cannot be computed ; the 'clear' area is present around the posterior upper apex. Distitarsi cordiform.

The claws appear entire at first sight but close inspection reveals a single tooth at about half-way down. Pulvillus well developed.

Remarks. In 1938 Armbruster criticized Roussy's description of these insects, which admittedly was in a popular style. He failed, however, to appreciate their significance since he was unacquainted with the *Trigona*-like group of *Electrapis*. The very detailed description here given will, it is hoped, fill an awkward gap and establish this group as a natural division of the primitive honey bees. (See also p. 254.)

Electrapis (Roussyana) proava (Menge 1856)

(Pl. 3, figs 3, 4)

*1856 *Apis proava* Menge : 26.
1891 *Apis proava* Menge ; Scudder : 689 (5938).
1907 *Apis proava* Menge ; Handlirsch : 892.
1909d *Apis proava* Menge ; Cockerell : 7.
1915 *Apis proava* Menge ; Buttel-Reepen : 10.
1928 *Apis proava* Menge ; Wheeler : 98.
1931 *Apis proava* Menge ; Statz : 40.
1931 *Apis proava* Menge ; Salt : 143.

Lectotype. British Museum (Natural History), In.43592, herein selected.

Paralectotype. British Museum (Natural History), In.18757.

Distribution. Eocene, Baltic amber.

Diagnosis. Body about 6 mm long (after some allowance has been made for a contracted and bent abdomen), length of forewing 6·5 mm. Scant hair on body as well as on eyes ; hind leg rather lanky, due to a proportionately long tibia, basitarsus broad, flat and rectangular, posterior edge convex ; wings hyaline, almost hairless.

Description. The lectotype, on which the following description is based, is well preserved, blackish in colour, with the terminal portion of thorax becoming paler, the whole body being very scantily supplied with hairs. The actual length of the body is 6 mm, length of abdomen approx. 2·25 mm, width of abdomen 2·25 mm; length of thorax approx. 2·75 mm, width of thorax 2·5 mm; length of hind tibia 3·25 mm.

Head squarish, poorly supplied with hair; ocelli prominent. Mouth parts not known. Antennae as recent *Apis*, but pedicel 'ball-shaped' and scape broadened distally, meeting the pedicel steeply.

Thorax proportionately very broad and thick, tapering sharply distally, not hairy, reminiscent of some species of *Trigona*.

The foreleg has an antenna cleaner of a somewhat primitive type, and well characterized by the clasp, which is long and thin and completely overlaps the hollow. The zone of articulation of tibia and tarsus is greatly extended.

The middle legs have a pronounced spur on the apex of the tibia. This spur is longer and sturdier than the corresponding spur of the hind leg. The outer edge of the tibia is well provided with hairs.

Hind legs fuscous, a little disproportionate on account of the great length of the tibia, the latter provided with long, somewhat plumose, hairs along the posterior edge and a neat row of short hairs down the inner median line. A single spur is present but its position is such that it is difficult to see on the specimen. Basitarsus rectangular, with convex posterior edge, covered with hairs which are strong on the inner side. An auricle is possibly not present but a concavity is present between tibia and basitarsus. One gains the impression that this zone is slightly more primitive than in *Electrapis* (*R.*) *palmnickenensis*. There is a tibial rake, which is stronger and coarser than that of the latter species.

The venation of the forewing is characterized as follows. Stigma comparatively large, vein cu-a at right angles on A and meeting Cu slightly distally of the junction with the basal vein. Upper section of basal vein (Rs) apparently proportionately longer than that of *E. meliponoides*.

Hindwing incompletely preserved. Eight hamuli, compared with six in *E.* (*R.*) *palmnickenensis*. One might be inclined to regard this as a meliponid feature, since *E.* (*E.*) *tornquisti* has 15, *E.* (*E.*) *meliponoides* 16 (though *E.* (*E.*) *apoides* has only 8), *Apis* (*Synapis*) *henshawi* has 17, Recent *A. mellifera* 20–23 and *A. dorsata* 23, but the smaller *A. florea* only 12. Recent *Bombus* species have 20–23 and *Euglossa* 27. There appears, however, to exist a relation between the number of hamuli, on the one hand, and body size and power of flight, on the other.

The part of the hindwing which is preserved includes cu-a, r-m and sections of M and Rs, together with cell Cu. It agrees with *E.* (*E.*) *apoides*.

The second specimen, In.18757, is covered with 'schimmel', and is assigned to *E.* (*R.*) *proava* with some reservation. It is larger than the lectotype, being 8·1 mm long. The forewing is 6·8 mm long and shows a dark apical cloud covering about one-twelfth of its area. The venation, in so far as it can be ascertained, appears to be identical with that of the lectotype. We hold that this is Menge's other specimen, as will be shown under 'Remarks'.

REMARKS. It appears that Cockerell (1909d) thought little of Menge's detailed description, and that he never saw the specimens, presumably because he expected them to be in the Koenigsberg Collection.

We have satisfied ourselves that the two specimens, In.43592 and In.18757 of the British Museum (Natural History), are in fact Menge's types, though no specific identification was attached to them. Our reasons are as follows. Two specimens were available to Menge, one almost entire and the other covered with 'schimmel', i.e. with the products of the gases of putrefaction. The first lends itself to description, but the second is in a very poor condition. Menge's description of the first tallies in a remarkable way with the British Museum specimen In.43592, and in a negative manner so does the second, In.18757. Furthermore, the history of the specimens supports this view. They were purchased in 1892 by the Trustees of the British Museum from Messrs Stantien & Becker, first placed in the Zoology Department and later (about 1904) transferred to the Department of Geology (now Palaeontology).

Fossil insects preserved in amber were sold by the above-mentioned firm over a long period of time. Their stocks were eventually taken over by the Prussian State and became the care of the State Amber Collection in Koenigsberg. Before this happened, however, Dr Richard Klebs, a geologist in the Prussian State Geological Survey, was in charge of the amber collection of Messrs Stantien & Becker. A set of 346 specimens were purchased by the British Museum in 1892, which included the two bees in question. These specimens bear labels marked 'R. Klebs, Museum Stantien & Becker'. This suggests that they did not come directly from the amber works of the firm, but were acquired through Dr Klebs. There is other evidence that not only the Menge Collection, but also part of the Germar and Berendt Collections was dispersed with the aid of this firm, and it would appear that Dr Klebs bought up such collections in the first instance and handed them over to the firm at a later date. For this reason specimens of such provenance are usually assigned to the 'Klebs Collection'.

If the specimens In.43592 and In.18757 were obtained by the British Museum in 1892 from Menge's collection *via* Dr Klebs and Messrs Stantien & Becker it is evident that Cockerell could not have found them in the Koenigsberg Collection in 1908.

It now remains to be shown that Menge's descriptions indeed tally with those given here as the result of independent study. Of the well-preserved specimen, Menge says that it is 7 mm long, with the wings 10 mm, breadth 3–4 mm. The abdomen is bent so that the sting lies under the apex of the tarsi of the first pair of legs. The tarsus of the foreleg comprises an antenna cleaner, or rather a sinus ('ausschnitt'). A spur is present on the tibia of the hind leg where it projects from its outer surface, and bristles are present on the digits of the hind feet. The bristles are a little irregularly shaped. The body itself is scantily haired and the ocelli and compound eyes are bare. The latter are oblong and narrow, and separated from each other. Twelve antennal segments are present, and these, together with the shape of the eyes, indicate for Menge a worker bee.

This description is at variance with our observations in two respects. First, the number of segments of the antennae of the fossil cannot be ascertained. Those of the good specimen (and the other is too obscured by 'schimmel' for any reliable observation) has one flagellum cut off short at the surface of the amber, the other twisted into a difficult position. Menge, however, referred to twelve visible segments for the worker.[9] The explanation of the discrepancy between descriptions and fossil is believed to be the treatment of the specimen whilst in the hands of Messrs Stantien & Becker. The amber pieces were reduced in size to the minimum, preferably made rectangular, and embedded in a resin in a glass cell on a microscope slide. The polishing process resulted in the loss of the distal portion of the antenna, and parts of the legs. Menge, therefore, may well have been able to study the entire antenna.

The second particular in which the description differs from the fossil is Menge's reference to the abdomen being so bent as to lie under the tarsi of the front pair of legs. The abdomen of the fossil does appear to be bent under the body but certainly not to such a forward position as Menge suggested. Also no sting can be seen. The abdomen, however, does touch the tarsus of a leg which must be one of the middle pair, for both fore and both hind legs can be made out separately. But the disposition of the abdomen is so obscured by the poor state of the amber in this region that it is possible for Menge to have made the above statement rather from conjecture than from actual observation, especially as he would have expected the abdomen to be longer than it actually is, believing the species to be closely related to *Apis mellifera*.

Though Menge was right in saying that the general morphology of the specimens resembles that of the honey bee in many respects, closer study has now revealed some features reminiscent of *Trigona*, such as the proportionately broad thorax, the short and round abdomen, and the small number of hamuli.

Genus ***APIS*** Linneaus 1758

*1758 *Apis* Linnaeus : 343, 575.
1810 *Apis* Latreille : 439.
1938 *Hauffapis* Armbruster : 43.

GENOTYPE. *Apis mellifera* Linnaeus 1758 (= *Apis mellifica* Linnaeus 1766), designated by Latreille (1810 : 439).

DIAGNOSIS. Medium-sized bees, with hair. Eyes usually hairy, clypeus not protuberant ; well-developed hind tibia, but spurs and comb lacking ; basitarsus rectangular and covered with bristles arranged in rows ; no reduction in wing venation, marginal cell always complete.

REMARKS. This genus comprises the Oligocene, Miocene and Recent Apini. They are all extremely closely related to each other, and the division into two subgenera is based on very unsatisfactory characters. Similarly, the numerous species and subspecies that have been named cannot all be maintained if the standard of Recent taxonomy is applied.

---

[9] This number is incorrect of course, for Recent *Apis* workers, if it refers to the flagellar segments, since it is the drone that has twelve and the queen and worker (females) eleven segments, but it was probably computed to include the scape.

Subgenus ***SYNAPIS*** Cockerell 1907

*1907 *Apis* (*Synapis*) Cockerell : 229.
1931 *Synapis* Cockerell ; Statz : 42.

GENOTYPE. *Synapis henshawi* Cockerell 1907, by monotypy.

DIAGNOSIS. General morphology very much like that of Recent *Apis* but differing in the following points : labrum less tongue-shaped ; third segment of flagellum short but broad ; basitarsus, though variable in shape, never identical with Recent *Apis* ; junction of veins cu-a, Cu and the basal vein coincident, or vein cu-a lies in a slightly more proximal position.

REMARKS. This group of honey bees has been extensively treated by Statz in 1931 and 1934, who regarded it as a genus. Cockerell, however, did not grant it more than subgeneric status, regarding the venation characters as important. Cockerell's view has been adopted by the present writers.

Apis (Synapis) cuenoti Théobald 1937

*1937 *Apis cuenoti* Théobald : 401 ; pl. 8, fig. 16, pl. 28, fig. 8.

HOLOTYPE. École des Eaux et Forêts, Nancy, No. F.173 (Coll. Fliche).

DISTRIBUTION. Oligocene (Stampian), Cereste, France.

DIAGNOSIS. Length of body 13·75 mm ; eyes pubescent ; hair on body fairly plentiful ; second m-cu meets M near distal corner of cell second Rs ; forewing length 12·5 mm.

REMARKS. Not so well preserved as some other representatives of *Synapis*. Specific rank has been retained for this specimen since it is most difficult to reconcile the wealth of hair, the pubescence of the eye (compare *A.* (*S.*) *henshawi kaschkei*, p. 243, the extraordinary length of the wing and the distal juncture of second m-cu with M, with any other *Synapis*. Théobald compared it with *Apis oligocenica* (recte *A.* (*S.*) *henshawi*), and suggested some connection between the two. It is thus likely that upon re-examination the specimen may turn out to resemble this species more closely than is at present apparent.

Apis (Synapis) henshawi Cockerell 1907

*1907 *Apis* (*Synapis*) *henshawi* Cockerell : 229.
1907 *Apis* (*Synapis*) *henshawi* Cockerell ; Handlirsch : 1357.
1915 *Apis oligocenica* Meunier : 210, pl. 21, fig. 4.
1915 *Apis henshawi* Cockerell ; Buttel-Reepen : 14.
1931 *Apis* (*Synapis*) *henshawi* Cockerell ; Statz : 42.
1934 *Synapis henshawi* Cockerell ; Statz : 3, 6, tf. 1, 4, 5, 6.
1934 *Apis oligocaenica* Meunier ; Statz : 1.
1938 *Apis oligocaenica* Meunier ; Armbruster : 88.

HOLOTYPE. Museum of Comparative Zoology, Harvard University.

DISTRIBUTION. Oligocene (Aquitanian), Rott, West Germany.

Diagnosis. Body 12–16 mm, forewing 8·5–10 mm. Variably hairy, eyes naked. Second m-cu meets base of cell second Rs on the abscissa of vein M beyond halfway.

Description. The three subspecies included in this species vary in size, the body being 12–16 mm. *A.* (*S.*) *cuenoti* would be included in this on the grounds of size, but its forewing is longer than in any known specimen of *A.* (*S.*) *henshawi*. The hairiness varies, and the hairs are perhaps sometimes plumose on the vertex. These bees closely resemble *A. mellifera* in general appearance.

Remarks. The first description of this species is by Cockerell (1907). He examined three specimens from Rott which the Museum of Comparative Zoology, Harvard, had obtained from the firm of Dr Krantz, Bonn, under the name of *Apis dormitans* Heyden 1862. One of these specimens was named *Synapis henshawi* by Cockerell, but since the other two bore *Apis dormitans* labels, he assumed that they belonged to Heyden's species, which Cockerell regarded as different from his *S. henshawi*.

Curiously enough, Heyden also had used three specimens of the Krantz Collection for his description of *Apis dormitans*, so that it seemed possible that Heyden's specimens were those that were eventually sold to Harvard University. That this is not so, however, is revealed by the fact that Cockerell was able to describe wings of all three Harvard specimens, whilst Heyden stated that one of his specimens was 'without visible signs of wings'. Moreover, the holotype of *Apis dormitans* Heyden is in the collection of the British Museum (Natural History), and its re-examination (p. 251) has confirmed the view held by other authors that Heyden's species is not an *Apis*.

Apis dormitans Cockerell (*nec* Heyden), based on two specimens in the Harvard Collection, is a true *Apis* (*Synapis*), as was demonstrated by Statz (1931). Hence it becomes necessary to rename this form, the species name being preoccupied by Heyden's form.

Three different *Synapis* have been described from Rott. They all come from the same beds and the same biotope. In view of the variation known to exist in large *Apis* populations, they are here reduced to subspecific status.

Apis (*Synapis*) *henshawi dormiens* subsp. nov.

(Pl. 4, figs 1–5)

*1907 *Apis dormitans* (*nec* Heyden) ; Cockerell : 228.
1908 *Apis dormitans* Cockerell ; Handlirsch : 1357.
1931 *Apis oligocenica* Meunier ; Statz : 46 (erroneously placed here).
1931 *Synapis dormitans* (Cockerell) ; Statz : 42, 46, figs 1a, 2b, 3c, 4a, 5–9.
1934 *Synapis dormitans* (Cockerell) ; Statz : 1, figs 2, 8, 10.
1944 *Synapis dormitans* (Cockerell) ; Statz : 63, figs 1, 3, 6.

Holotype. Museum of Comparative Zoology, Harvard University. (Cockerell's first specimen, 1907, described as *Apis dormitans*.)

Paratype. Second specimen ; Museum of Comparative Zoology, Harvard.

Material studied. In addition to the holotype and paratype, two specimens in the British Museum (Natural History), Nos 59634 and In.36655; also all the specimens in the collection of Dr Statz, Cologne.

Distribution. Oligocene (Aquitanian): Rott.

Diagnosis. Body 13 mm, forewing 8·5 mm. Hair on vertex not plumose, eyes naked. Basitarsus with 9 rows of bristles, middle row numbering 24. Vein cu-a a little proximad of junction of basal vein with Cu.

Description. The medium-sized form of the species. In addition to the characters stated in the diagnosis, the following are worth noting: the flagellum is not narrowed at the base, the basitarsus is 1·6 mm long and 0·9 mm wide and the depstum only moderately developed.

Remarks. Numerous other specimens exist, mostly collected by Dr Statz, to whom we owe the detailed description and excellent reproduction of specimens. In 1931 Statz thought that Meunier's *Apis oligocenica* was synonymous with his *Synapis dormitans*, but after the study of Meunier's type he correctly synonymized it with *S. henshawi* (q.v.).

Apis (Synapis) henshawi henshawi Cockerell 1907

*1907 *Apis* (*Synapis*) *henshawi* Cockerell: 229.
1915 *Apis oligocenica* Meunier: 210.
1934 *Synapis henshawi* Cockerell; Statz: 5, figs 1, 4, 5, 6, 7.
1944 *Synapis henshawi* Cockerell; Statz: 63, figs 2, 5.

Holotype. Museum of Comparative Zoology, Harvard University.

Other material. Holotype of *Apis oligocenica* Meunier, Heimatmuseum, Siegburg an der Lahn. Five specimens in the Statz Collection.

Distribution. Oligocene (Aquitanian): Rott.

Diagnosis. Body 15–16 mm, forewing 10 mm. Hair on vertex plumose or simple, eyes naked. Basitarsus with 10 rows of bristles (second very short), middle row numbering about 28. Vein cu-a coincident with junction of basal vein with Cu.

Description. This is the largest of the three subspecies. Making allowance for the distended abdomen (measured length 16·5 mm), Cockerell inferred a length of 15 or 16 mm. When Statz encountered the holotype of *Apis oligocenica* Meunier in the Siegberg Museum, he satisfied himself that it was conspecific with *A.* (*S.*) *henshawi*, and he described it in detail under that name in 1934. There appears indeed to be a close agreement between Cockerell's and Meunier's types, except that Statz states positively that the hair on the vertex is not plumose, whilst in Cockerell's specimen 'this hair appears to be plumose'. Evidently, Cockerell did not feel quite sure, and since the hair is simple in all other *Synapis*, he may have misinterpreted his specimen.

The wings are strikingly short for the size of the body. The antenna cleaner is deeply incised, semicircular, and thus differs from the shallower type present in *A.* (*S.*) *dormiens*. The basitarsus has ten rows of bristles, whilst in *A.* (*S.*) *dormiens* only nine appear to be present, and the number of bristles comprising the middle rows is slightly larger.

Apis (Synapis) henshawi kaschkei (Statz 1931)

*1931 *Synapis kaschkei* Statz : 50, figs 10, 11.
1934 *Synapis kaschkei* Statz ; Statz : 3, figs 3, 9.

HOLOTYPE. In Statz Collection, Cologne.

DISTRIBUTION. Oligocene (Aquitanian) : Rott.

DIAGNOSIS. Body 11–12 mm, forewing 9·25 mm. Basitarsus broad, and shorter than in any known *Apis*. Vein cu-a very proximad of junction of basal vein with Cu.

DESCRIPTION. This is the smallest bee from Rott. It differs from the other two *Synapis* in the structure of the basitarsus which is very short and almost square (1·2 mm long and 1·0 mm broad). Statz, in saying that this basitarsus almost agrees with that of *Apis iridiae* Friese from Sumatra, is, however, mistaken, as this species has a pronouncedly oblong basitarsus. The depstum closely resembles that of Recent *Apis mellifera* Linn., but the wing venation places this form in the genus *Synapis*. There appear to be nine rows of bristles on the basitarsus, including the second row which is very short. It has a smaller body and a longer forewing than the other two *Synapis*.

REMARKS. Only three specimens are known, two of which, including the holotype, have been seen by one of us. Its status may have to be reconsidered when more material becomes known. For the time being, Statz's description cannot be improved upon. He figures the holotype (1931 : figs 10, 11) and a second specimen in his own collection (1934 : figs 3, 9), the latter figure being the diagram of the forewing venation derived from the two forewings of this specimen.

Subgenus ***APIS*** Linnaeus 1758

*1758 *Apis* Linnaeus : 343, 375.
1938 *Hauffapis* Armbruster : 43 (Genotype : *Hauffapis scheuthlei* Armbruster).

GENOTYPE. *Apis mellifera* Linnaeus 1758 (= *Apis mellifica* Linnaeus 1766), designated by Latreille (1810 : 439).

DIAGNOSIS. Third segment of flagellum shorter, but not broader, than the remaining segments ; the broadly rectangular, neatly curved basitarsus always possesses a distinct auricle ; cross vein cu-a well proximad of the junction of basal vein and Cu.

REMARKS. This subgenus contains, apart from *Apis mellifera,* with its race *A. m. indica* Fabr., the large *Apis dorsata* Fabr. of India and the small *A. florea* Fabr. of India.

The fossil forms from the Pleistocene belong to the *A. mellifera* group, and those from the Miocene also are rather closer to this Recent species than to either of the other two.

Apis (Apis) armbrusteri Zeuner 1931

1929 'Scheuthle Biene' Armbruster : 4.
1931 'Scheuthle Biene' Statz : 44, 46.
*1931 *Apis armbrusteri* Zeuner : 1292, fig. 21, pl. 8, fig. 1.
1938 *Hauffapis scheuthlei* Armbruster : 43, 92, figs 1–5, 7, 8, 14, 20, 23, 26, 29, 33, 35, 38–40, 51, 53, 55, 58, 63–65, 67, 70–72, 76, 77, 79.

HOLOTYPE. Württembergische Naturaliensammlung, Stuttgart, Boettingen Collection No. 47, individual No. 3 (head, thorax and abdomen). Cast : British Museum (Natural History) In.38859 (thorax) and In.38856 (abdomen).

PARATYPES. Württembergische Naturaliensammlung, Stuttgart, Boettingen Collection No. 47, individuals Nos 1, 2, 4–17. Casts : British Museum (Natural History) In.38857 (thorax, No. 1), In.38858 (thorax, No. 2), In.38860 (thorax, No. 4).

OTHER MATERIAL. The specimens described by Armbruster (1938) from the Upper Miocene of the Randecker Maar, all here attributed to *Apis armbrusteri* as a species. Subspecific distinctions have, however, been retained as will be seen below.

DISTRIBUTION. Upper Miocene, Württemberg.

DIAGNOSIS. A bee resembling *Apis mellifera* in size and appearance, with wax mirrors on the abdomen, the posterior edges of the sternites being apparently straight. Wings proportionately slightly broader than in the Recent species, position of the junction of the second m-cu with M, and shape of the first m-cu variable.

REMARKS. In 1931, one of us (F. E. Z.) described a fossil swarm of honey bees from the thermal limestone of Böttingen on the Swabian Alb, Württemberg, under the name *Apis armbrusteri.* It had perished in peculiar circumstances, having fallen into a fissure, on the edge of the crater of an Upper Miocene volcano, from which a spring was issuing and which released carbon dioxide into the atmosphere. Whilst these specimens afforded many details of the body structure, the wing venation could not be studied.

After the termination of the eruptions, but still in the Upper Miocene, lakes had formed in the rather larger crater of the Randecker Maar which is situated in the same volcanic area. Shales deposited in these lakes produced an abundant insect fauna, again probably because either the water or the atmosphere was temporarily poisoned. In 1926 Wilhelm Scheuthle discovered bees here.

In 1928 he was joined by Professor Armbruster, and their search resulted in the recovery of a very large number of specimens which, however, were not scientifically described until 1938, under the names of *Hauffapis scheuthlei*, *H. scheeri* and *H. scharmanni* Armbruster, with a number of subspecies. These bees provide valuable information about venation, being compressed in much the same way as the bees from Rott. The variation observed is great, but no clear line can be drawn justifying the maintenance of species. It is altogether very unlikely that in an area of 50 miles there should have existed simultaneously four hardly distinguishable species of honey bees with four more subspecies. On geographical, stratigraphical and morphological grounds, therefore, the Böttingen and Randeck bees should be regarded as one variable species. The specific names given by Armbruster have been allotted subspecific rank, as they may be useful in the discussion of the variation, whilst Armbruster's subspecies have been synonymized with his species. In essence, this appears to represent not only ours, but Professor Armbruster's views, who in 1938 stated that he considered the Randeck bees identical with *Apis armbrusteri* Zeuner. The new names were perhaps, in part, prompted by his wish to honour some of his collaborators and colleagues.

All specimens so far recovered at Randeck and Böttingen are workers, except for a single fragment of a drone from Randeck. The following four subspecies may be distinguished.

Apis (Apis) armbrusteri armbrusteri Zeuner 1931

*1931 *Apis armbrusteri* Zeuner : 292, fig. 21, pl. 8, fig. 1.
1934 *Apis armbrusteri* Zeuner ; Statz : 7.
1938 *Apis armbrusteri* Zeuner ; Armbruster : 16, 45.

HOLOTYPE AND PARATYPES. See under species, above.

DISTRIBUTION. Miocene, 'Böttinger Marmor', Böttingen, Swabian Alb, Württemberg.

DIAGNOSIS. Head 2 mm, thorax 5 mm, abdomen 12 mm (distended). Mesothorax strongly vaulted, middle segment only slightly sloping. First abdominal segment very short, vertical and concave anteriorly. Posterior edges of abdominal sternites not or very little angular at mid-line.

DESCRIPTION. On a piece of red tufa measuring not more than 45 ×35 ×10 mm, 17 individuals are preserved in a layer and in a closely packed condition. The insects appear as undistorted cavities and have to be studied with the aid of casts made in an elastic material. The cavities have been broken in various positions, the abdomina (being the largest) being available most frequently. In addition, 5 thoraces and 3 heads can be studied.

Head. The eyes appear to have been oval, not kidney-shaped. They are separated on the vertex, hence the specimens may be regarded as workers.

Thorax. Almost spherical, strongly vaulted above. Prothorax short, the shoulder-buckles not reaching the tegulae. Shoulder-buckles prominent laterally in an angular fashion. Mesopleurae curved, about twice as high as long. Middle coxae long and fitted into the thorax, not pointing obliquely backwards, but vertical to the longitudinal axis of the insect. Mesonotum very strongly vaulted, more so than in *A. mellifera*, and exceeding the scutellum in height. Scutellum sharply set off and forming a prominent crosswise flange. Middle segment sloping at a smaller angle than in *A. mellifera* or even in *A. florea*.

Abdomen. Stalk short, first segment concave anteriorly, short, as seen from above. The posterior margins of the middle sternites are not angular, but more or less straight. After careful investigation, this could not be attributed to distension or distortion of the abdomen ; it thus appears to be a sound diagnostic character. Wax mirrors present.

REMARKS. The Böttingen bees differ from the three Recent species of *Apis* in the shape of the thorax, whose mesonotum is so strongly vaulted that it exceeds the scutellum in height, a feature that may be interpreted as a sign of high specialization. Similarly, the shape of the first abdominal segment suggests specialization beyond the level of *Apis mellifera*. In other respects, however, the Böttingen bees are more primitive than *A. mellifera*, especially in the shape of the abdominal sternites, and perhaps in the slight slope of the middle segment of the thorax.

It is much to be regretted that no evidence could be obtained about the collecting apparatus or the hind legs. Attempts made to expose the legs by carefully grinding away the matrix proved unsuccessful.

A. armbrusteri was a social bee which in all probability lived much like *A. mellifera*. The wax mirrors suggest that combs were built of this substance as is characteristic of the genus *Apis*. The fact that 17 individuals were contained in a closely packed condition in the small piece of rock recovered suggests that a much larger number of bees perished and were fossilized, a swarm which would have fallen into the death trap of the Böttingen fissure and perished almost instantaneously in its poisoned atmosphere.

Apis (Apis) armbrusteri scharmanni (Armbruster 1938)

*1938 *Hauffapis scharmanni* Armbruster : 44, 113, fig. 78.

HOLOTYPE. Armbruster's specimen and fig. no. 78, in the collection of Dr Hauff, Holzmaden.

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Approx. 9·1 mm long ; form compact ; head massive ; abdomen plump ; corbicula (tibia) very broad but short, much reduced at base ; apex of 'pollen kneader' (counterpart of auricle, on the tibia) strong and angular ; wax mirrors elongated and hammer-shaped ; vein first R_1 possibly not arched.

DESCRIPTION. This is a small bee though the respective states of preservation have to be taken into consideration in comparing it with *A. armbrusteri armbrusteri*. The edge of the tibia, from pollen kneader to the end of the limb, forms almost a straight line, as in *A. a. scheuthlei*. Second Rs (third submarginal cell) not narrowed unduly ; second m-cu joining base of third submarginal cell more towards the middle ; cubital basis (according to Armbruster) as long as the corbicula, but reputed to be shorter than in *A. a. scheeri* ; first m-cu only a little deflected ; Cu_1 straight. The tergites of the abdomen are very narrow but very long.

REMARKS. This is in several respects a curious bee and of the several forms here discussed the one perhaps most deserving of specific rank. Unfortunately the type appears to be lost ; Armbruster had to use 'photograms' as a substitute for the specimen. Other photographs mentioned by the author appear to be of the same specimen, and no paratypes are known to exist.

Apis (Apis) armbrusteri scheeri (Armbruster 1938)

*1938 *Hauffapis scheeri* Armbruster : 43, 92, figs 50, 52, 62, 64, 66, 69, 71, 73.
1938 *Hauffapis scheeri* var. *gallauni* Armbruster : 45, figs 31, 59.
1938 *Hauffapis scheeri* var. *rahdei* Armbruster : 45, fig. 50.

LECTOTYPE. Schempp Collection, Stuttgart-Weil (Armbruster 1938 : fig. 71), herein selected.

PARALECTOTYPES. Collections of Scheuthle and Schempp.

OTHER MATERIAL. Holotypes of *Hauffapis scheeri gallauni* Armbruster, No. 59 and of *Hauffapis scheeri rahdei* Armbruster, No. 50.

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Smaller, plumper than *A. a. scheuthlei*, with narrower third submarginal cell, and relatively short, broad and boldly formed hind tibia and basitarsus. Legs very reminiscent of those of Recent *A. mellifera*.

DESCRIPTION. Short dense hair, partly arranged in lines, occurring on the abdomen. The wax mirrors are long and narrow. The first m-cu is distinctly angular in the holotype. In most respects this form resembles *A. mellifera* greatly, and especially in the shape and size of the wing, and in certain details of the venation. The length of the body varies ; a giant form was given the name of *H. s. gallauni* and a dwarf form *H. s. rahdei*. There is also much variation in overall size and proportions. Armbruster gave the average length of the cubital basis as 2·96 mm, though he illustrated specimens in which this measurement is 3·05, 3·2 and 3·3 mm, which thus appears to be of little taxonomic value.

REMARKS. Of this very variable subspecies, 24 specimens have been recorded. Of these, three are only doubtfully placed here. The total includes the 'giant' and 'dwarf' forms to which Armbruster gave special names.

Apis (Apis) armbrusteri scheuthlei (Armbruster 1938)

1929 'Scheuthle Biene' ; Armbruster : 4.
1931 *Apis* sp. ; Zeuner : 296.
*1938 *Hauffapis scheuthlei* Armbruster : 43, figs 63, 65, 67, 70, 72, 76, 77, 79.
1938 *Hauffapis scheuthlei* var. *seemanni* Armbruster : 45, figs 8, 11, 21, 26, 53.
1938 *Hauffapis scheuthlei* var. *zeuneri* Armbruster : 45, figs 36, 38.

LECTOTYPE. W. Scheuthle Collection (Armbruster 1938 : fig. 63), herein selected.

PARALECTOTYPES. Armbruster, Scheuthle, Schempp and Hauff Collections.

OTHER MATERIAL. Holotype of *Hauffapis scheuthlei seemanni* (Armbruster Coll. no. 8), and paratypes (nos 11, 21, 26, 53). Holotype of *Hauffapis scheuthlei zeuneri* (Armbruster Coll. no. 36), paratype (same collection, no. 28).

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Larger than *A. a. scharmanni* and *A. a. scheeri*, size slightly exceeding *A. mellifera* except in dwarf specimens. Third submarginal cell broader than in *A. a. scheeri*. Legs slender, somewhat resembling those of *A. dorsata*.

Description. This is the largest of the three forms of bees from Randecker Maar here recognized. Though the majority of the specimens are of the size of large Recent *A. mellifera*, giant and dwarf forms have been described. *A. s.* var. *seemanni* is a giant form, whilst the smallest specimens were named *A. s.* var. *zeuneri*. The body is covered in hair which is somewhat coarse.

Compared with *A. a. scheeri*, the legs of *A. a. scheuthlei* are longer and more slender. The hind tibia (corbicula), considered by Armbruster to be slightly curved in outline, is less narrow towards the base. The basitarsus, too, has a straighter outline. Armbruster is inclined to regard the legs as reminiscent of *A. dorsata*.

The first submarginal cell of the forewing often appears arched to meet C ; the second and third submarginal cells are broader than in *A. a. scheeri* ; pterostigma much reduced ; the first recurrent vein is markedly angular, with a small stump of a vein at the apex of the angle.

Remarks. Armbruster distinguished two subspecies, *A. s. seemanni* and *A. s. zeuneri*. These are here synonymized with *A. a. scheuthlei* as they are merely extreme size variants which would be found in any large population. Regarding one of the specimens assigned to *A. s. seemanni* (no. 35), Armbruster (1938 : 103–4) assigned its counterpart to *A. a. scheuthlei* (no. 33) and withdrew the identification of no. 35 (1938 : 114), without, however, altering the text on the earlier pages. That this should have been possible illustrates how small the difference is between these size classes.

Armbruster attached some importance to the length of the cubital basis, i.e. the base vein of cells first R_1, first Rs and second Rs. He did so presumably because it is a measure that can be taken on a comparatively large number of wings, including those the total length of which cannot be measured. In *A. a. scheuthlei* this cubital basis is reputed to equal the length of the corbicula. In fact it varies from 3·06 to 3·40 mm. In his *A. s. seemanni*, the value is 3·67 mm. Of *A. s. zeuneri* no measurements are given, except for no. 64 (Scheuthle Coll.) which is regarded as possibly referable to this form. Here it is ‘apparently hardly longer than 3·0 mm’. The unreliability of this measurement has been clearly demonstrated by Alber (1949), who studied the asymmetry of the wings of bees.

Altogether 44 specimens have been assigned to this variable ‘species’, which Armbruster regarded as ‘possibly, nay even probably’ overlapping with *Apis armbrusteri* Zeuner. The wax mirrors are preserved on many of the Randecker Maar specimens, but their shape is not discussed. From the figures it appears that the margins of the sternites were more or less straight, and the wax mirrors rectangular, as in the Böttingen form.

Apis (Apis) melisuga (Handlirsch 1907)

*1907 (Apidae) *melisuga* Handlirsch : 893.

Holotype. Collection of Count Bosnianski, with counterpart ; whereabouts unknown.

Distribution. Miocene, Gabbro, Italy.

Diagnosis. 18 mm long. Other features believed to be much as in *Apis mellifera.*

Description. Proboscis at least as long as head. Hind leg with distinct bristles along the edges. Venation not identifiable.

Remarks. The broadened hind tibia and tarsus strongly suggest a true *Apis.* It is impossible to decide, however, how far it resembles the Recent *A. dorsata*, or differs from *A. a. scheuthlei.* It is, therefore, retained as a separate species, in the hope that fresh material will become available in the future.

Apis (Apis) mellifera Linnaeus 1758

(Pl. 4, fig. 6)

*1758 *Apis mellifera* Linnaeus : 343, 575.
1890 *Apis mellifica* Linnaeus ; Foord : 94, fig. 1.
1909c *Apis mellifera* Linnaeus ; Cockerell : 317.

Specimens studied. British Museum (Natural History), Palaeontology Dept., 58516, 58576.

Distribution. Pleistocene, East African copal.

Description. The specimens here listed from East African copal do not differ from Recent *A. mellifera* in any essential point. Body length of specimen no. 58576 is 11 mm ; thorax 3·25 mm long and 4 mm wide ; abdomen 6 mm long and 4 mm wide. Length of wings 8·75 mm.

Remarks. Several honey bees are known from the copal of East Africa. Foord (1890) mentioned two specimens side by side. His poor figure suggests the shape of the basitarsus being identical with *A. mellifera.*

Cockerell (1909c) examined two specimens from the Cambridge Collection. They were at first believed to be enclosed in Yarmouth amber and hence to be of Eocene age, but he considered it much more likely that sailors had brought them from East Africa for the Yarmouth trade in amber fossils.

Specimen no. 58576 has been studied in detail. Its wing venation is remarkable in two respects ; the first submarginal cross vein (first abscissa of Rs) is S-shaped, and vein first m-cu (first recurrent) appears to lack the usual angularity. The peculiar shape of the submarginal cross vein is known also in *Synapis*, as well as in *A. florea* and to a lesser extent in *A. dorsata.* One might, therefore, regard it as a primitive character, but since it occurs also in a specimen of *A. mellifera* from Entebbe, Uganda, it appears to have persisted in some East African bees. The lack of angularity of first m-cu is believed to be a mere accident of preservation ; angularity indeed probably does exist, though it may not be very marked, and it is masked in this specimen by a slight fold in the wing.

The abdomen of the East African copal bee has yellow bands, like its modern counterpart.

Family **APIDAE** ***incertae sedis***

'Apis' aquitaniensis de Rilly 1930

*1930 *Apis aquitaniensis* de Rilly (not seen).
1931 Abeille mellifère ; Alphandéry : 3, fig. on p. 3.
1938 *Apis aquitaniensis* de Rilly ; Armbruster : 88.
1950 *Apis aquitaniensis* de Rilly ; de Rilly : 45.

Holotype. Muséum Marseille, No. 5979, as stated by both Armbruster (1938) and Roussy (personal communication). Repeated enquiries, however, have not succeeded in eliciting its present whereabouts.

Distribution. Oligocene (Aquitanian) : Aix-en-Provence.

Diagnosis. Length of body 16 mm, length of thorax 5 mm, length of abdomen 9 mm, length of forewing 10 mm, length of hind leg 7·5 mm.

Description. According to Alphandéry, two antenna are visible on the head, and one eye is well preserved. The rest of the head is badly crushed but its general shape is triangular, like heads of bees with mandibles in general. The thorax is also crushed and has a black depression in the centre. On its edges there are two orange-coloured ridges. The left wing is beautifully spread and shows all the characteristics of a honey bee. The third pair of legs is well spread out, and the tibia shows a broadening suggestive of a pollen basket. Five abdominal segments can be distinguished.

This description is an almost literal translation from Alphandéry (1931).

Remarks. This specimen was first mentioned in an article by F. de Rilly (1930) entitled *L'abeille fossile française*, of which nothing further is known. It may be identical with an article said to have been written by that author in 1924, which we have not seen either. Alphandéry's description is vague. His reference to the left wing showing 'all the characteristics of the honey bee' is perplexing when applied to an Oligocene species, and his figure is useless. Armbruster, aware of this, was fortunate enough to receive a facsimile in coloured plastic from F. de Rilly. This, however, was scarcely the likeness of an *Apis*.

Through the kindness of Monsieur Roussy we have been able to inspect a similar facsimile and we agree with Armbruster's conclusion. But the question arises as to whether the fault lies with the facsimile.

A paper by de Rilly (1950) appears to answer this question. In it he asserts once again his claim that the specimen under discussion is an *Apis*, but with 'quelques caractères archaïques (cellule supplémentaire de l'aile, éperon tibial)'. According to an enlargement of the wing (published in 1924) and reproduced in facsimile, however, the supplementary cell is that formed by a cross vein to the marginal cell, which is thus a cell completely unknown in Apidae. Moreover, the pterostigma is exceptionally large and deep. The éperon-tibial, which undoubtedly belongs to the hind tibia (since the tibial spur of the middle leg, being always present in *Apis*, affords no diagnostic character) is worth something, in that it rules out the genus *Apis* proper. The few positive indications which have been made available in de

Rilly's work (1950) prove that this specimen is not an *Apis*, and probably not even a member of the Apidae.

'*Apis*' *dormitans* Heyden 1862

*1862 *Apis dormitans* Heyden : 76, pl. 10, fig. 8.
1891 *Apis dormitans* Heyden ; Scudder : 689 (5927).
1907 *Apis dormitans* Heyden ; Cockerell : 228.
1907 *Apis dormitans* Heyden ; Handlirsch : 892.
1908 *Apis dormitans* Heyden ; Handlirsch : 1357.
1915 *Apis* (?) *dormitans* Heyden ; Buttel-Reepen : 13.
1915 *Osmia dormitans* (Heyden) ; Buttel-Reepen : 14.
1915 *Apis dormitans* Heyden ; Meunier : 210.
1931 *Osmia dormitans* (Heyden) ; Statz : 42.
1931 *Apis dormitans* Heyden ; Statz : 42.

HOLOTYPE. British Museum (Natural History), 58778.

DISTRIBUTION. Oligocene (Aquitanian) : Rott am Siebengebirge.

REMARKS. According to Carl von Heyden three specimens existed but the first was very poorly preserved and he was far from happy about placing it in the genus *Apis*. The second and third specimens were too meagrely described for recognition. Buttel-Reepen considered that the whole habitus, the rounding off of the abdomen and the great breadth of the thorax compared with the breadth of the head, indicated, not an *Apis*, but an *Osmia*. Meunier considered it to be some kind of worker bee, but referred to it as a very enigmatical form. All authors agree that it has not been proved to be an *Apis*.

The re-examination of the holotype, which was damaged by water during the war, confirms the views of previous authors. No character is preserved which would justify placing it in *Apis*, and the rounded end of the abdomen precludes it from being included in this genus. The venation, which Heyden also shows in his figure, is too poor for generic identification.

Two further specimens of '*A. dormitans*', from Rott, now in the Museum of Comparative Zoology, Harvard University, were investigated by Cockerell (1907). They are specifically different from the specimens referred to above but are legitimate members of *Apis* (*Synapis*). Hence they require a new name, and have been described as *Apis* (*Synapis*) *henshawi dormiens* n. subsp. (p. 241).

'*Apis*' *styriaca* Pongrácz 1931

*1931 *Apis styriaca* Pongrácz : 105.
1938 *Apis styriaca* Pongrácz ; Armbruster : 88.

HOLOTYPE. Whereabouts not known.

DISTRIBUTION. Miocene : Parschlug.

REMARKS. A wing fragment only has been referred to, but not described. Its affinities are wholly obscure, and the name must be treated as a *nomen nudum*.

'Bombus' carbonarius Menge 1856

1856 *Bombus* Latreille ; Menge : 26.
*1856 *Bombus carbonarius* Menge : 27.
1886 *Bombus* Latreille ; Brischke : 278.
1891 *Bombus carbonarius* Menge ; Scudder : 690 (5950).
1907 *Bombus carbonarius* Menge ; Handlirsch : 891.
1909d *Bombus carbonarius* Menge ; Cockerell : 5.
1928 *Bombus carbonarius* Menge ; Wheeler : 97.
1931 *Bombus carbonarius* Menge ; Salt : 143.

Distribution. Eocene : Baltic amber.

Remarks. Apparently Menge had five specimens in two blocks of amber, but only two species were present, which he called *B. carbonarius* and *B. pusillus*. No diagnosis or description was ever published.

'Bombus' muscorum Roussy 1937

non 1935a *Bombus muscorum* (Linnaeus) ; Richards : 73.
*1937 *Bombus muscorum* Roussy : 58.

Distribution. Eocene : Baltic amber.

Holotype. Whereabouts unknown.

Description. A solitary bee, red and black, and abundantly hairy. No further details.

Remarks. Cannot be assigned to any genus on the characters given.

'Bombus' pusillus Menge 1856

1856 *Bombus* Latreille ; Menge : 26.
*1856 *Bombus pusillus* Menge : 27.
1891 *Bombus pusillus* Menge ; Scudder : 691 (5954).
1907 *Bombus pusillus* Menge ; Handlirsch : 891.
1909d *Bombus pusillus* Menge ; Cockerell : 5.
1928 *Bombus pusillus* Menge ; Wheeler : 96.

Distribution. Eocene : Baltic amber.

Remarks. See *'Bombus' carbonarius* Menge above.

'Bombus' antiquus Heyden 1859

*1859 *Bombus antiquus* Heyden : 12, pl. 2, fig. 4.
1862 *Bombus antiquus* Heyden ; Heyden : 75.
1891 *Bombus antiquus* Heyden ; Scudder : 690, pl. 31, fig. 4 (5949).
1907 *Bombus antiquus* Heyden ; Handlirsch : 891.
1931 *Bombus antiquus* Heyden ; Cockerell : 309.
1936 *Bombus antiquus* Heyden ; Statz : 260.

Holotype. Whereabouts now unknown. Originally in von Dechen's collection.

Distribution. Oligocene (Aquitanian) : Rott am Siebengebirge.

Remarks. Specimen lacking several parts and even Heyden (1862) considered it 'perhaps not different from *Osmia carbonum*', thus making its generic status very insecure. There is no useful purpose served in synonymizing it with the latter species, since Heyden's statement is far too casual, and possibly had little real significance. No subsequent author has considered the specimen to be 'good'.

'Bombus' grandaevus Heer 1849

*1849 *Bombus grandaevus* Heer : 96, pl. 7, figs 3a, b.
1856 *Bombus grandaevus* Heer ; Giebel : 182–183.
1867 *Bombus grandaevus* Heer ; Heer : 5, pl. 3, figs 6, 7.
1891 *Bombus grandaevus* Heer ; Scudder : 690 (5952).
1895 *Bombus grandaevus* Heer ; Scudder : 122.
1907 *Bombus grandaevus* Heer ; Handlirsch : 891.
1928 *Bombus grandaevus* Heer ; Wheeler : 97.
1931 *Bombus grandaevus* Heer ; Cockerell : 309.
1938 *Bombus grandaevus* Heer ; Armbruster : 87.

Holotype. Badische Landessammlung für Naturkunde, Karlsruhe. Not traced. (Heer 1849 : fig. 3.)

Another specimen. As figured by Heer (1867).

Distribution. Miocene : Radoboj.

Remarks. Cockerell regarded this form as generically unclassifiable. Scudder thought it was not a *Bombus*, but possibly belonging to *Eucera*. Handlirsch (1907) also believed that it belonged near *Eucera* but to a new genus. Heer's illustrations provide no help. They suggest, however, that two different specimens were in existence, those figured in 1849 and 1867.

We have made enquiries at Karlsruhe and visited the Museum, but the specimens cannot be found. It is possible they may come to light when the material packed away in the cellars during the war is sorted out.

'Bombusoides' mengei Motschulsky 1856

*1856 *Bombusoides Mengei* Motschulsky : 28.
1891 *Bombusoides mengei* Motschulsky ; Scudder : 691 (5955).
1907 *Bombusoides mengei* Motschulsky ; Handlirsch : 892.
1909d *Bombusoides mengei* Motschulsky ; Cockerell : 5.
1928 *Bombusoides mengei* Motschulsky ; Wheeler : 97.

Distribution. Eocene : Baltic amber.

Description. A bumble bee not more than 1½ lines (3·175 mm) long. No further description provided.

Remarks. On formal grounds this is the genotype of *Bombusoides* Motschulsky. The holotype is lost. The size given is much too small for any bumble bee.

Apidae gen. et sp. indet. 1 (Brischke)

1886 *Bombus* Latreille ; Brischke : 278.
1891 *Bombus* Latreille ; Scudder : 690 (5946).
1907 *Bombus* Latreille ; Handlirsch : 891.

Distribution. Eocene : Baltic amber.

Remarks. A single '*Bombus*' mentioned but not described. Probably either *B. carbonarius* Menge or *B. pusillus* Menge, both *nomina nuda* (p. 252).

Apidae gen. et sp. indet. 2 (Brischke)

1886 *Melipona* Brischke : 278.
1891 *Melipona* (vic.) Brischke ; Scudder : 716 (6175).
1896 *Melipona* Tosi : 356.
1907 *Melipona* (vic.) Brischke ; Handlirsch : 892.

Distribution. Eocene : Baltic amber.

Description. 'Venation is reminiscent of the South American genus *Melipona* but differs in the structure of the legs.'

Remarks. Two specimens appear to have been known to Brischke, but the described specimens are now lost. The comparison with *Melipona* means little in view of the existence of the meliponoid *Electrapis*.

Apidae gen. et spec. indet. 3 (Burmeister)

1832 *Trigona* Burmeister : 636.
1836 *Trigona* Burmeister : 577.
1856 *Trigona* Burmeister ; Giebel : 184.
1891 *Trigona* (?) Burmeister ; Scudder : 733 (6324).
1896 *Trigona* Tosi : 356.
1907 *Trigona* (?) Burmeister ; Handlirsch : 892.

Distribution. Eocene : Baltic amber.

Remarks. Perhaps identical with *Electrapis* (*Roussyana*) *palmnickenensis* (p. 233). Specimen lost.

Apidae gen. et sp. indet. 4 (Scudder)

1881 *Bombus* Scudder : 290.
1883 *Bombus* Scudder : 280.
1891 *Bombus* Scudder : 690 (6947).
1907 *Bombus* Scudder ; Handlirsch : 891.

Distribution. Oligocene : Florissant.

Remarks. One of the specimens of bees which Scudder knew from Florissant was assigned to *Bombus* without further description or comment.

NOT APIDAE

Lithoblatta lithophila (Germar 1839)

*1839 *Musca lithophila* Germar : 222.
1864 *Blattidium beroldingianum* Heer : 300, fig. 8.
1869 *Musca lithophila* Germar ; Weyenbergh : 256, pl. 34, fig. 2 (no. 6511).
1869 *Bombus* (?) *conservatus* Weyenbergh ; Weyenbergh : 259, pl. 34, fig. 7.
1869 *Apiaria veterana* Weyenbergh ; Weyenbergh : 260, pl. 34, fig. 8 (no. 6480 *nec* 6431).
1886 *Mesoblattina lithophila* (Germar) ; Scudder : 464.
1886 *Mesoblattina lithophila* (Germar) ; Deichmüller : 6, pl. i, figs 1–6.
1888 *Mesoblattina lithophila* (Germar) ; Oppenheim : 221, pl. 30, figs 6, 8.
1895 *Mesoblattina lithophila* (Germar) ; Meunier : 223.
1898 *Mesoblattina lithophila* (Germar) ; Meunier : pl. 25, figs 76–78 ; pl. 26, figs 85–86 ; pl. 27, figs 92–93.
1898 *Naucoris carinata* Meunier : pl. 27, fig. 88.
1907 *Lithoblatta lithophila* (Germar) ; Handlirsch : 530, pl. 46, fig. 7.
1931 *Bombus conservatus* (Weyenbergh) ; Cockerell : 309.

HOLOTYPE. Whereabouts not known, probably lost.

SPECIMENS STUDIED. Teyler Museum, Haarlem, Netherlands, No. 15324 (*Bombus conservatus*) and No. 15305 (*Apiaria veterana*).

DISTRIBUTION. Upper Jurassic : Solnhofen, Bavaria.

REMARKS. Meunier regarded both *B. conservatus* and *A. veterana* as cockroaches (*Mesoblattina*). His view was shared by Handlirsch who identified them with Germar's *Musca lithophila* and erected the new genus *Lithoblatta*. Thus the supposed bees of the Upper Jurassic have proved to be Orthoptera.

The specimens in Haarlem which we have studied support this view. No. 15324 has an orthopteroid habitus, and No. 15305 has long antennae and orthopteroid tibia. Cockerell, who saw *B. conservatus*, also held that it is 'wholly obscure and there is no reason for regarding it as a bee'.

VI. APPENDIX

by S. F. Morris

Colletidae gen. et sp. indet.

1927 Colletidae ; Blair : 139.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. According to Blair the material is 'perhaps Upper Pliocene, perhaps Quaternary or probably Sub-recent'. Oil sands ; near Fyzabad, Trinidad.

Ctenoplectrella splendens Kelner-Pillault 1970

*1970a *Ctenoplectrella spendens* Kelner-Pillault : 13, pl. 1, figs 3, 4.

MATERIAL. Holotype : Geologisch-palaeontologischen Institut der Universität, Göttingen. Paratype : No. 49, Zoologisches Museum der Humboldt-Universität, Berlin.

DISTRIBUTION. Eocene, Baltic amber.

Anthidiini gen. et sp. indet.

1972 Anthidiini ; Sando : 424.

Material. Gerard Germs Collection.

Distribution. Recent (collected from rocks of Precambrian and Lower Palaeozoic age).

Osmia sp.

1972 *Osmia* sp. ; Sando : 421.

Material. United States National Museum ; United States Geological Survey, Glacier National Park Museum ; Harvard University, Paleobotany Collection.

Distribution. Recent (in rocks of Precambrian to Upper Palaeozoic age), Montana, Wyoming.

Apoidea (? Anthophorinae) sp.

1969 Apoidea (? Anthophorinae) sp. ; Werner : 12, pl. 19, fig. 3.

Material. United States National Museum 257, B.218.

Distribution. Early Pleistocene, Rita Blanca lake deposits.

Probombus hirsutus Piton (ms)

1940 *Probombus hirsutus* Piton (ms) : 218.
1969b *Probombus hirsutus* Piton ; Kelner-Pillault : 526 (*nomen nudum*).

Distribution. Eocene, Menat, Puy-de-Dôme, France.

Trigona (Hypotrigona) eocenica Kelner-Pillault 1970

*1970b *Trigona* (*Hypotrigona*) *eocenica* Kelner-Pillault : 437, figs 1–3.

Material. Holotype : Geologisch-palaeontologischen Institut der Universität, Göttingen. Paratype formerly in the Geological Museum of the University, Königsburg ; now in the Humboldt Museum, Berlin.

Distribution. Eocene, Baltic amber.

Trigona (Hypotrigona) dominicana Wille & Chandler 1964

*1964 *Trigona* (*Liotrigona*) *dominicana* Wille & Chandler : 188, figs 1–5.

Material. Holotype and five paratypes in the collection of the Illinois Natural History Survey.

Distribution. Oligocene, Dominican Republic.

Trigona (Nogueirapis) silacea Wille 1959

*1959 *Trigona* (*Nogueirapis*) *silacea* Wille : 849, pl. 119, text-figs 1–4.
1964 *Trigona* (*Nogueirapis*) *silacea* Wille ; Wille : 120, fig. 1.

MATERIAL. Holotype : 12601. Paratypes : 12602–11. In University of California Museum.

DISTRIBUTION. Middle Miocene, Simjovel, Chiapas Province, Mexico.

Electrapis minuta Kelner-Pillault 1970

*1970a *Electrapis minuta* Kelner-Pillault : 16, pl. 2, figs 3, 5B.

MATERIAL. Syntypes : Geologisch-palaeontologischen Institut der Universität, Göttingen ; Block 50a, Zoologisches Museum der Humboldt-Universität, Berlin.

DISTRIBUTION. Eocene, Baltic amber.

Apis catanensis Roussy 1960

*1960 *Apis catanensis avolii* Roussy : 8, fig. 2.
1969b *Apis catanensis avolii* Roussy ; Kelner-Pillault : 524.

MATERIAL. One specimen in the private collection of Anastasi and Guiseppe Avolio, jewellers of Sicily.

DISTRIBUTION. Miocene, near Catania, Sicily.

REMARKS. Roussy used the trinomen *Apis catanensis avolii*, but since the species was not split the third name is superfluous.

? **Apoidea** sp.

1821 Vast numbers of bees and nests ; Henslow : 501.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. Parish of Kirk Balaft, Isle of Man ; ? Pleistocene.

Not Apoidea

1962 Native bee ; Carroll : 264, fig. 1.

MATERIAL. Melbourne University, Geological Dept., M.U.G.D. 3518.

DISTRIBUTION. ? Lower Jurassic, Koonwarra, South Gippsland, Victoria, Australia.

VII. ACKNOWLEDGEMENTS

The task of an amanuensis is a difficult one, but to undertake the publication of a manuscript on a subject with which one is unfamiliar, and whose authors one did not work with or even know, requires a particular courage and dedication. Thus,

great credit is due to Mr S. F. Morris for his initiative in revivifying the manuscript and in undertaking much of the editorial work towards its publication. Thanks are also due to Mr D. L. F. Sealy who prepared the paper for the press, and to Professor O. W. Richards for his advice.

H. W. Ball
Keeper of Palaeontology

VIII. REFERENCES

[Although every effort has been made to trace all the references cited in the text, in a few cases, indicated below by *, this has unfortunately not been possible; though bibliographic references can be given in most instances, they must be cited as 'not seen' (by the Editor). It is evident that some works which were available to the authors are not now to be obtained in any British library. The Editor gratefully acknowledges the assistance of the librarians of the British Museum (Natural History) in his efforts to trace the missing works. Though not cited in the text, references marked † are known to have been consulted by the authors during the preparation of this paper. They are included as a contribution to the general bibliography of the subject. S. F. M.]

Alber, M. 1949. Asymmetrie der Bienenflügel. *Arch. Bienenk.*, Berlin, **26** : 14–16.

*Alphandéry, E. 1931. *Traité complet d'apiculture.* vi + 572 pp. Paris.

Armbruster, L. 1929. Wilhelm Scheuthle †. *Bienenpflege*, Württemberg, **51** (1) : 5–8.

*—— 1938. Versteinerte Honigbienen aus dem obermiocänen Randecker Maar. *Arch. Bienenk.*, Berlin, **19** : 1–48, 97–133, figs 1–79.

Ashmead, W. H. 1899. Classification of the Bees, or the Superfamily Apoidea. *Trans. Am. ent. Soc.*, Philadelphia, **26** : 49–100.

Bequaert, J. C. & Carpenter, F. M. 1941. The antiquity of social insects. *Psyche, Camb.* **48** : 50–55.

Berthold, A. A. 1827. *Latreille's naturliche Familien des Thierreichs.* viii + 602 pp. Weimar.

†Bischoff, H. 1927. *Biologie der Hymenopteren.* 598 pp. Berlin.

Blair, K. G. 1927. Insect Remains from Oil Sand in Trinidad. *Trans. ent. Soc. London* **75** : 137–141.

Brischke, D. 1886. Die Hymenopteren des Bernsteins. *Schr. naturf. Ges. Danzig* (n.f.) **6** (3) : 278–279.

Brown, R. W. 1934. *Celliforma spirifer*; the fossil larval chambers of mining bees. *J. Wash. Acad. Sci.*, Menasha, **24** : 532–539, 5 figs.

—— 1935. Further notes on fossil larval chambers of mining bees. *J. Wash. Acad. Sci.*, Menasha, **25** : 526–528.

—— 1941a. The comb of a wasp nest from the Upper Cretaceous of Utah. *Am. J. Sci.*, New Haven, **239** : 54–56, 1 pl.

—— 1941b. Concerning the antiquity of social insects. *Psyche, Camb.* **48** : 105–110.

Burmeister, C. H. C. 1832. *Handbuch der Entomologie* **1**. xvi + 698 pp., 16 pls. Berlin.

—— 1836. *A manual of Entomology.* xii + 654 pp., 33 pls. London.

†Buttel-Reepen, H. von 1903. *Die Stammesgeschichtliche Entstehung des Bienenstaates sowie Beiträge zur Lebensweise der solitären und sozialen Bienen.* 138 pp., 20 figs. Leipzig.

—— 1906. Apisticae. Beiträge zur Systematik, Biologie, sowie zur geschichtlichen und geographischen Verbreitung der Honigbiene (*Apis mellifica* L.), ihrer Varietäten und der übrigen Apis-Arten. *Mitt. zool. Mus. Berl.* **3** : 117–201, 8 figs.

—— 1915. *Leben und Wesen der Bienen.* 300 pp. Brunswick.

Buxton, P. A. 1932. Ancient workings of insects, perhaps bees, from Megiddo, Palestine. *Proc. ent. Soc. Lond.* **7** (1) : 2–4.

Carroll, E. J. 1962. Mesozoic fossil insects from Koonwarra, South Gippsland, Victoria. *Aust. J. Sci.*, Sydney, **25** : 264–265, 2 figs.

Cockerell, T. D. A. 1900. Observations on bees collected at Las Vegas, New Mexico, and in the adjacent mountains. *Ann. Mag. nat. Hist.*, London, (7) **5** : 401–416.

—— 1906. Fossil Hymenoptera from Florissant, Colorado. *Bull. Mus. comp. Zool. Harv.* **50** : 33–58.

—— 1907. A Fossil Honey-Bee. *Entomologist*, London, **40** : 227–229.

—— 1908a. Descriptions and Records of Bees, 19. *Ann. Mag. nat. Hist.*, London, (8) **1** : 337–344.

—— 1908b. Descriptions and Records of Bees, 20. *Ann. Mag. nat. Hist.*, London, (8) **2** : 323–334.

—— 1908c. A fossil leaf-cutting bee. *Can. Ent.*, Ottawa, **40** : 31–32.

—— 1908d. Some results of the Florissant expedition of 1908. *Am. Nat.*, Salem, Mass., **42** : 569–581, 12 figs.

—— 1909a. Two fossil bees. *Ent. News*, Philadelphia, **20** : 159–161.

—— 1909b. A Catalogue of the Generic Names based on American Insects and Arachnids from the Tertiary Rocks with Indications of the Type Species. *Bull. Am. Mus. nat. Hist.*, New York, **26** : 77–86.

—— 1909c. Some European Fossil Bees. *Entomologist*, London, **42** : 313–317.

—— 1909d. Descriptions of Hymenoptera from Baltic Amber. *Schr. phys.-ökon. Ges. Königsb.* **50** : 1–20, 14 figs.

—— 1909e. New North American Bees. *Can. Ent.*, Ottawa, **41** : 393–395.

—— 1909f. Some Additional Bees from Prussian Amber. *Schr. phys.-ökon. Ges. Königsb.* **50** : 21–25.

—— 1911a. Fossil insects from Florissant, Colorado. *Bull. Am. Mus. nat. Hist.*, New York, **30** : 71–82.

—— 1911b. Descriptions and Records of Bees, 34. *Ann. Mag. nat. Hist.*, London, (8) **7** : 225–237.

—— 1913a. Some fossil insects from Florissant, Colorado. *Proc. U.S. natn. Mus.*, Washington, **44** : 341–346, pl. 56.

—— 1913b. Some fossil insects from Florissant. *Can. Ent.*, Ottawa, **45** : 229–233.

—— 1914. Miocene fossil insects. *Proc. Acad. nat. Sci. Philad.* **66** : 634–648, 5 figs.

—— 1917. New Tertiary insects. *Proc. U.S. natn. Mus.*, Washington, **52** : 373–384, pl. 31.

—— 1921. Fossil Arthropods in the British Museum. *Ann. Mag. nat. Hist.*, London, (9) **8** : 541–545, 5 figs.

—— 1922. Fossils in Burmese Amber. *Nature, Lond.* **109** : 713–714.

—— 1923. Two Fossil Hymenoptera from Florissant (Vespidae, Megachilidae). *Ent. News*, Philadelphia, **34** : 270–271.

—— 1925a. Descriptions and Records of Bees, 106. *Ann. Mag. nat. Hist.*, London, (9) **16** : 416–423.

—— 1925b. Tertiary insects from Kudia River, Maritime Province, Siberia. *Proc. U.S. natn. Mus.*, Washington, **68** (5) : 1–16, pls 1–2.

—— 1931. Insects from the Miocene (Latah) of Washington, II. Hymenoptera and Hemiptera. *Ann. ent. Soc. Am.*, Washington, D.C., **24** : 309–312, pl. 1, figs 2, 4, 8.

—— 1934. Some African Meliponine Bees. *Revue Zool. Bot. afr.*, Brussels, **26** : 46–62, 9 figs.

Curtis, J. 1828. *British Entomology* **5** : pls 195–241 with explanations. London.

Dall, W. H. 1915. A monograph of the molluscan fauna of the *Orthaulax pugnax* zone of the Oligocene of Tampa, Florida. *Bull. U.S. natn. Mus.*, Washington, D.C., **90** : 1–173, pls 1–26.

†Dalla Torre, K. W. von & Friese, H. 1899. Die hermaphroditen und gynandromorphen Hymenopteren. *Ber. naturw.-med. Ver. Innsbruck* **24** : 96 pp., 1 pl.

Daly, H. V. 1973. Bees of the Genus *Ceretina* in America North of Mexico (Hymenoptera : Apoidea). *Univ. Calif. Publs Ent.*, Berkeley, **74** : 1–114, 2 pls.

Deichmüller, J. V. 1886. Die Insecten aus dem lithographischen Schiefer im Dresdener Museum. *Mitt. K. miner.-geol. prähist. Mus. Dresden* **7** : 1–88, pls 1–5.

Dours, R. Z. 1873. Hyménoptères du Bassin Méditerranéen. *Revue Mag. Zool.*, Paris, (3) **1** : 274–325.

Fabricius, J. C. 1775. *Systema entomologiae.* 30+832 pp. Flensburg and Leipzig.

—— 1805. *Systema Piezatorum.* 439+30 pp. Brunswick.

Foord, A. S. 1890. Notes on a collection of East Coast amber belonging to Mrs Burwood of Yarmouth. *Trans. Norfolk Norwich Nat. Soc.* **5** : 92–95, 1 pl.

†Friese, H. 1923. *Die europaischen Bienen* (*Apidae*). 456 pp., 33 pls. Berlin and Leipzig.

Germar, E. F. 1839. Die versteinerten Insecten Solenhofens. *Nova Acta physico-med.*, Breslau and Bonn, **19** (1) : 187–222, pls 21–23.

—— 1849. Ueber einige Insekten aus Tertiärbildungen. *Z. dt. geol. Ges.*, Berlin, **1** : 52–66, pl. 2.

Giebel, C. G. 1856. *Fauna der Vorwelt mit stäter Berücksichtigung der lebenden Thiere.* 511 pp. Leipzig.

Handlirsch, A. 1906–8. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* 1430 pp., 51 pls.

†—— 1921. *In* Schröder, C., *Handbuch der Entomologie* **3** (7) : 117–304, figs 52–327. Jena.

Heer, O. 1849. Die Insektenfauna der Tertiargebilde von Oeningen und von Radoboj. *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.*, Zurich, **11** : 1–264.

†—— 1850. Die Insektenfauna der Tertiargebilde von Oeningen und von Teningen und von Radoboj in Croatien, II. *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.*, Zurich, **11** : 264 pp., 17 pls.

—— 1864. Ueber die fossilen Kakerlaken. *Vjschr. naturf. Ges. Zürich* **9** : 273–302, 1 pl.

—— 1865. *Die Urwelt der Schweiz.* 622 pp., 11 pls, 368 figs. Zurich.

—— 1867. Fossile Hymenopteren aus Oeningen und Radoboj. *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.*, Zurich, **22** : 1–42, 3 pls.

—— 1872. *Le Monde primitif de la Suisse.* 801 pp., 11 pls, 368 figs. Geneva and Basle.

—— 1876. *The Primaeval World of Switzerland,* **2**. 324 pp., 11 pls, 370 figs. London.

—— 1879. *Die Urwelt der Schweiz.* 2nd (rewritten and enlarged) ed. xix+713 pp., 12 pls, 417 figs. Zurich.

Henslow, J. S. 1821. Supplementary observations to Dr. Berger's account of the Isle of Man. *Trans. geol. Soc. Lond.* **5** : 482–505.

Heyden, C. von 1859. Fossile Insekten aus der Rheinischen Braunkohle. *Palaeontographica*, Cassel, **8** : 1–15, pls 1–2, figs 1–13.

—— 1862. Gliedertiere aus der Braunkohle des Niederrhein's, der Wetterau und der Röhn. *Palaeontographica*, Cassel, **10** : 62–82, pl. 10.

Hünefeld, L. 1831. Derselbe über Bernsteininsecten. *Isis, Leipzig* **15** : col. 1100 (numb. in error 2000). [Determinations by C. H. C. Burmeister.]

†Jack, R. W. 1917. Parthenogenesis amongst the Workers of the Cape Honey Bee : Mr G. W. Onions' Experiments. *Trans. ent. Soc. London* **49** : 396–403, pls 105–106.

†Jones, F. W. 1943. *Habit and Heritage.* 100 pp. London.

Jurine, L. 1807. *Nouvelle méthode de classer les Hymenoptères et les Diptères* **1**. 319 pp., 14 pls. Geneva.

†Kelner-Pillault, S. 1968. Les Abeilles fossiles. *13th Int. Congr. Ent., Proc.*, Moscow, **1** : 256.

—— 1969a. Abeilles fossiles ancêtres des Apides sociaux. *Proc. VI Congr. IUSSI*, Berne : 85–93.

—— 1969b. Les abeilles fossiles. *Memorie Soc. ent. ital.*, Genoa, **48** : 519–534, 10 figs.

—— 1970a. L'ambre balte et sa faune éntomologique avec déscription de deux Apoides nouveaux. *Annls Soc. ent. Fr.*, Paris (n.s.) **6** : 3–24, 6 figs.

—— 1970b. Une Mélipone (s.l.) de l'Ambre balte (Hym. Apidae). *Annls Soc. ent. Fr.*, Paris, (n.s.) **6** : 437–441, 3 figs.

Kerr, W. E. & Maule, V. 1964. Geographical distribution of stingless bees and its implications (Hymenoptera : Apidae). *Jl N.Y. ent. Soc.*, New York, **72** : 2–8, 4 figs, 6 maps.

Kirby, W. 1802. *Monographia Apum Angliae* **1**. xxii+258 pp., 14 pls. Ipswich.

Kohl, F. F. 1894. Zur Hymenopterenfauna Afrikas. *Annln naturh. Mus. Wien* **9** : 279–350, pls 13–17.

Latreille, P. A. 1802a. *Histoire naturelle des Fourmis, et recueil de mémoires et d'observations sur les Abeilles, les Araignées, les Fauchers, et autres Insectes.* xvi + 445 pp., 12 pls. Paris.

†—— 1802b. *Histoire naturelle, générale et particulière des Crustacés et des Insectes* **3**. 468 pp. Paris.

—— 1803. *Nouveau Dictionnaire d'Histoire Naturelle* **18**. 595 pp., pls 23–33. Paris.

—— 1804. *Nouveau Dictionnaire d'Histoire Naturelle* **24**. Tableaux Méthodiques .... 238 pp. Paris.

—— 1809. *Genera Crustaceorum et Insectorum* **4**. 399 pp. Paris.

—— 1810. *Considérations générales sur l'ordre naturel des Animaux composant les classes des Crustacés, des Arachnides, et des Insectes ; avec un Tableau méthodique de leurs genres, deposés en familles.* 444 pp. Paris.

—— 1825. *Familles naturelles du Règne Animal, exposées succinctement et dans un ordre analytique avec l'indication de leurs genres.* 570 pp. Paris.

Lea, A. M. 1925. Notes on some calcareous insect puparia. *Rec. S. Aust. Mus.*, Adelaide, **3** : 35–36, 1 pl.

Lepeletier de Saint-Fargeau, A. L. M. 1841. *Histoire naturelle des Insectes. Hyménoptères*, **2**. 680 pp. Paris.

—— & Audinet-Serville, J. G. 1828. *In* Latreille, P. A., *Encyclopédie méthodique. Histoire naturelle* **10**. 833 pp. Paris.

†Leuenberger, F. 1931. Eine fossile Biene. *Schweiz. Bienenztg*, Aarau, **3** : 3 pp., 1 fig.

Linnaeus, C. 1758. *Systema naturae* .... 10th edition, **1**. 824 pp. Holmiae.

Magretti, P. 1884. Risultati di raccolte imenotterologische nell'Africa orientale. *Annali Mus. civ. Stor. nat. Giacomo Doria*, Genoa, **21** : 523–636, pl. 1.

—— 1895. Imenotteri. *Annali Mus. civ. Stor. nat. Giacomo Doria*, Genoa, **35** : 149–173, 4 figs.

Malfatti, G. 1881a. Bibliografia degli Insetti fossili Italiani finora conosciuti. *Atti Soc. ital. Sci. nat.*, Milan, **24** : 89–100.

†—— 1881b. Due piccoli imenotteri fossili dell'Ambra siciliana. *Atti Accad. Lincei Transunti*, Rome, (3) **5** : 80–83, 2 figs.

†Manning, F. J. 1952. Recent and fossil honey bees : some aspects of their cytology, phylogeny and evolution. *Proc. Linn. Soc. Lond.* **163** : 3–8, 1 pl.

—— 1960. A new fossil bee from Baltic amber. *11th Int. Congr. Ent., Verh.*, Vienna, **1** : 306–308, pl. 5, fig. 1.

Menge, A. 1856. Lebenszeichen vorweltlicher, im Bernstein eingeschlossener Thiere. *Programm . . . öffentlichen Prüfung der Schüler der Petrischule* : 1–32. Danzig.

Meunier, F. 1895. Note sur des empreintes d'Insectes des schistes de Solenhofen. *Bull. Soc. ent. Fr.*, Paris, **64** : ccxxiii–ccxxiv.

—— 1898. Les insectes des temps secondaires. *Archs Mus. Teyler*, Haarlem, (2) **6** : 89–149, pls 1–30.

—— 1914. Nouvelles recherches sur quelques Insectes du Sannoisien d'Aix-en-Provence. *Bull. Soc. géol. Fr.*, Paris, (4) **14** : 187–198, pls 6–7, text-figs 1–11.

—— 1915. Über einige fossile Insekten aus den Braunkohlenschichten (Aquitanien) von Rott (Siebengebirge). *Z. dt. geol. Ges.*, Berlin, **67** : 205–217, pls 21–25, 6 figs.

—— 1920. Quelques insectes de l'Aquitanien de Rott, Sept-Monts (Prusse rhénane). *Proc. Sect. Sci. K. ned. Akad. Wet.*, Amsterdam, **22** : 727–737, 2 pls, 8 figs.

Michener, C. D. 1944. Comparative external morphology, phylogeny and a classification of the bees (Hymenoptera). *Bull. Am. Mus. nat. Hist.*, New York, **82** : 151–326, 246 figs.

—— 1965. A classification of the bees of the Australian and South Pacific regions. *Bull. Am. Mus. nat. Hist.*, New York, **130** : 1–362, 789 figs, 15 pls.

Motschulsky, V. 1856. Lettres . . . à M. Ménétriés, 3. *Étud. ent.*, Helsinki, **5** : 3–38, 1 pl.

Moure, J. S. 1961. A Preliminary Supra-specific Classification of the Old World Meliponine Bees (Hymenoptera, Apoidea). *Studia ent.*, Rio de Janeiro, **4** : 181–242.

NOVAK, O. 1877. Fauna der Cyprisschiefer des Egerer Tertiärbeckens. *Sber. Akad. Wiss. Wien* **76** : 71–96, pls 1–3.

OPPENHEIM, P. 1888. Die Insectwelt des lithographischen Schiefers in Bayern. *Palaeontographica,* Cassel, **34** : 215–247, pls 30–31.

OUSTALET, M. E. 1870. Recherches sur les insectes fossiles des terrains tertiaires de la France. *Annls Sci. géol. Paris* **2** (3) : 1–178, pls 1–6.

PANZER, G. W. F. 1806. *Kritische Revision der Insektenfauna Deutschlands* **2**. *Entomologischer Versuch die Jürineschen Gattungen der Linnéschen Hymenoptern nach dem Fabriciusschen System zu prüfen.* 271 pp., 2 pls. Nuremburg.

PITON, L. 1940. *Paléontologie du gisement éocène de Menat.* Thèse, Clermont-Ferrand.

†PLATH, O. E. 1934. *Bumblebees and their Ways.* 201 pp., 10 pls. New York.

PONGRÁCZ, A. 1928. Die fossilen Insekten von Ungarn. *Annls hist.-nat. Mus. natn. hung.*, Budapest, **25** : 91–194, 55 figs.

—— 1931. Bemerkungen über die Insektenfauna von Oeningen nebst Revision der Heer'schen Typen. *Verh. naturh.-med. Ver. Heidelb.* **17** : 104–125, pls 3–11.

†RICHARDS, O. W. 1935a. *Bombus muscorum* (Linnaeus) and *B. smithianus* White (Hym.). *Trans. Soc. Br. Ent.*, Southampton, **2** : 73–85, pl. 5.

—— 1935b. Notes on the nomenclature of the Aculeate Hymenoptera, with special reference to British genera and species. *Trans. R. ent. Soc. Lond.* **83** : 143–176.

*RILLY, F. DE 1930. L'abeille fossile française. *Apiculteur.* [Not seen by authors.]

*—— 1950. [title ?] *Ruchers* (10) : 45.

RODECK, H. G. 1938. Type specimens of fossils in the University of Colorado Museum. *Univ. Colo. Stud. gen. Ser.*, Boulder, **25** : 281–304.

ROSELLI, F. L. 1939. Apuntes de geología y paleontología Uruguayas y sobre insectos del Cretáceo del Uruguay o descubrimentos de admirables instintos constructivos de esa época. *Boln Soc. Amig. Cienc. nat. Kraglievich-Fontana*, Nueva Palmira, **1** (2) : 32–102, 32 figs.

ROSS, H. H. 1936. The ancestry and wing venation of the Hymenoptera. *Ann. ent. Am.*, Washington, D.C., **29** : 99–111, 2 pls.

*ROUSSY, L. 1937. Flore et Faune de l'ambre fossile de la Mer Baltique. *Gaz. apic.*, Montfavet, **388** : incl. p. 66 & fig. 13 (March 1937).

—— 1960. Insectes et abeilles fossiles de l'ambre de Sicile. *Gaz. apic.*, Montfavet, **635** : 5–8, 2 figs.

SALT, G. 1931. Three Bees from Baltic Amber. *Bernstein-Forsch.*, Berlin and Leipzig, **2** : 136–147.

SANDHOUSE, G. A. 1943. The type species of the genera and subgenera of bees. *Proc. U.S. natn. Mus.*, Washington, **92** : 519–668.

SANDO, W. J. 1972. Bee-nest pseudofossils from Montana, Wyoming and South-West Africa. *J. Paleont.*, Tulsa, **46** : 421–425, fig. 1.

SCHLETTERER, A. 1891. Hymenoptera in expeditione sub auspicio regii imperii Belgici perfecta in regione Africae ad Congo flumen inferius collecta, determinata sive descripta ab. *Annls Soc. ent. Belg.*, Brussels, **35** : 1–36, pls 1–2.

SCHMIEDEKNECHT, O. 1930. *Die Hymenopteren Nord- und Mitteleuropas.* x + 1062 pp., 127 figs. Jena.

SCHRÖDER, C. 1913–25. *Handbuch der Entomologie* **3**. viii + 1201 pp., 1040 text-figs. Jena. [See Handlirsch 1921.]

†SCHULZ, W. A. 1907. Alte Hymenoptera. *Berl. ent. Z.* **51** : 303–333.

SCHÜTZE, E. 1907. *In* Branca, W. & Fraas, E., Die Lagerungsverhältnisse Bunter Breccie an der Bahnlinie Donauwörth-Treuchtlingen und ihre Bedeutung für das Riesproblem. *Phys. Math. Abh. K. Akad. Wiss. Berlin* **2** : 25–26, 1 pl., figs 22–23.

SCHWARZ, H. F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. *Bull. Am. Mus. nat. Hist.*, New York, **90** : 1–546, pls 1–8, 87 figs.

SCUDDER, S. H. 1881. The tertiary lake basin at Florissant, Colorado, between South and Hayden Parks. *Bull. U.S. geol. geogr. Surv. Territ.*, Washington, **6** : 279–300.

Scudder, S. H. 1883. The tertiary lake basin at Florissant, Colo., between South and Hayden Parks. *Rep. U.S. geol. geogr. Surv. Territ.*, Washington, **12** : 271–293.

—— 1885. Myriopoda, Arachnoidea und Insecta. *In* Zittel, K. A., *Handbuch der Palaeontologie* : 723–893, figs 894–1109. Munich and Leipzig.

—— 1886. A Review of Mesozoic Cockroaches. *Mem. Boston Soc. nat. Hist.* **3** : 439–485, pls 46–48.

—— 1887. Partie 1, Mollusca et Arthropoda. *In* Zittel, K. A., *Traité de Paléontologie* **2**. 897 pp., 1126 figs. Paris, Munich and Leipzig.

†—— 1890. A classed and annotated bibliography of fossil insects. *Bull. U.S. Geol. Surv.*, Washington, **69** : 101 pp.

—— 1891. Index to the known fossil insects of the world including myriapods and arachnids. *Bull. U.S. Geol. Surv.*, Washington, **71** : 744 pp.

—— 1895. The Miocene Insect-fauna of Oeningen, Baden. *Geol. Mag.*, London, (4) **2** : 116–122, pl. 6.

Smith, F. 1854. *Catalogue of Hymenopterous Insects in the . . . British Museum* **2** : 199–465. London.

—— 1858. Catalogue of the Hymenopterous Insects. *J. Proc. Linn. Soc.*, London, **2** : 42–130, pls 1, 2.

Snodgrass, R. E. 1935. *Principles of Insect Morphology.* ix + 667 pp., 319 figs. London.

Spinola, M. 1808. *Insectorum Liguriae species novae aut rariores*, . . . [&c.] **2**. ii + 262 + v pp., 5 pls. Genoa.

—— 1838. Compte-rendu des Hyménoptères, recueillis par M. Fischer pendant son voyage en Égypte. *Annls Soc. ent. Fr.*, Paris, **7** : 437–546.

Stadelmann, H. 1895. Beiträge zur Kenntniss der Gattung *Melipona sens. lat. Sber. preuss. Akad. Wiss.*, Berlin, Jahrg. **1895** : 615–623, 3 figs.

Statz, G. 1931. Eine neue Bienenart aus Rott am Siebengebirge. *Wiss. Mitt. Ver. Natur-u. Heimatk. Köln* **1** : 39–60.

—— 1934. Neue Beobachtungen über fossile Bienen aus dem Tertiär von Rott am Siebengebirge. *Arch. Bienenk.*, Berlin, **15** (1) : 1–10, 10 figs.

—— 1936. Ueber alte und neue fossile Hymenopterenfunde aus den tertiären Ablagerungen von Rott am Siebengebirge. *Decheniana*, Bonn, **93** : 256–312, pls 1–13.

*—— 1943. Bienen, Blätter und Blüten dem rheinischen Braunkohlenwald. *Rhein. Heimatphl.*, Düsseldorf, **13** (for 1941) : 100–112, 14 figs. Also (same title) *Dtsch. Imkerführer* **16** (for 1942) : 6 pp., 22 figs. [These works, not seen by the authors, are *desiderata* in that they may contain new taxonomic names.]

*—— 1944. [title ?] *Umschau*, Frankfurt-a.-M., **48** (4) : 63, figs 2, 5.

Théobald, N. 1937. *Les insectes fossiles des terrains oligocènes de France.* 473 pp., 29 pls. Nancy.

Timon-David, J. 1943. Première étude des Insectes fossiles oligocènes du basin de Marseille. *C. r. hebd. Séanc. Acad. Sci., Paris*, **216** : 455–457.

—— 1944. Insectes fossiles de l'Oligocène inférieur des Camoins (Bassin de Marseille) II. Hymenoptères. *Bull. Soc. ent. Fr.*, Paris, **49** : 40–45, 5 figs.

Tosi, A. 1896. Di un nuovo genere di Apiaria fossile nell'ambra di Sicilia (Meliponorytes succini–M. sicula). *Rev. ital. Paleont.*, Bologna, **2** : 352–356, pl. 6, 9 figs.

Viereck, H. L. 1912. Contributions to our Knowledge of Bees and Ichneumon-flies, including twenty-one new genera and fifty-seven new species of Ichneumon-flies. *Proc. U.S. natn. Mus.*, Washington, **42** : 613–648, 2 figs.

Werner, F. G. 1969. *In* Anderson, R. Y. & Kirkland, D. W., Terrestrial insects of the Rita Blanca lake deposits. *Mem. geol. Soc. Am.*, Washington, **113** : 123–130, pl. 19.

Weyenbergh, H. 1869. Sur les insectes fossiles du calcaire lithographique de la Bavière, que se trouvent au Musée Teyler. *Archs Mus. Teyler*, Haarlem, **2** : 247–294, pls 34–37.

Wheeler, W. M. 1926. *Les sociétés d'insectes ; leur origine, leur évolution.* 468 pp., 61 figs. Paris. [English translation 1928.]

†Whiting, P. W. 1935. Sex determination in bees and wasps. *J. Hered.*, Washington, **26** : 229.

Wille, A. 1959. A new fossil stingless bee (Meliponini) from the amber of Chiapas, Mexico. *J. Paleont.*, Tulsa, **33** : 849–852, pl. 119, figs 1–4.

—— 1964. Notes on a primitive stingless bee, *Trigona* (*Nogueirapis*) *mirandula*. *Revta Biol. trop.*, San José, **12** : 117–151, 21 figs.

—— & Chandler, L. C. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera ; Meliponini). *Revta Biol. trop.*, San José, **12** : 187–195, 5 figs.

Zeuner, F. E. 1931. Die Insektenfauna des Böttinger Marmors. *Fortschr. Geol. Palaeont.*, Berlin, **9** : 247–406, pls 1–19.

—— 1938. Die Insektenfauna des Mainzer Hydrobien-kalks. *Palaeont. Z.*, Berlin, **20** : 104–151, pls 13–17.

—— 1944. Fossil Honey-Bees. *Brit. Bee-Keep. Ass.*, London : 10.

—— 1951. A Discussion of Time-rates in Evolution. *Proc. Linn. Soc. Lond.* **162** : 124-130.

IX. INDEX

New taxonomic names and the page numbers of the principal references are printed in **bold** type.

Aix-en-Provence 250
amber, see Baltic, Burmese, Sicilian
Andrena **165–6**, 167–9, 171, 175
  clavula **166**, 167
  grandipes **166**, 167
  hypolitha **166**, 167
  lagopus **167**
  percontusa **167**
  primaeva **167–8**, 183 ; pl. 1, fig. 2
  sepulta 166, **167**
  tertiaria 202
  wrisleyi **166**
  spp. indet. **168–9**
Andrenidae **165**, 166–71
Andreninae **165**, 166–70
Anthidiini 178, **256**
Anthidium **178**, 179
  curvatum 179
  exhumatum **179**
  mortuum **178–9**, 193
  scudderi **179**
Anthophora 193, **194**, 198, 204–5
  effossa 200, 202
  melfordi **194** ; pl. 1, fig. 1.
Anthophoridae **187**, 188–99
  gen. et spp. indet. **200**
  gen. et sp. indet. 256
Anthophorinae **192**, 193–9, 256
Anthophorini 192, **193**, 194–9
Anthophorites 193, **194–5**, 196–9
  gaudryi **195**, 197
  longaeva (*longaevus*) **195–6**
  mellona 193–5, **196–7**
  melona 196
  parietaria 195
  thoracica (*thoracicus*) **195**
  titania **197–8**
  tonsa (*tonsus*) **198**
  veterana (*veteranus*) **198–9**
ants 202, 219
Apiaria dubia **186**
  veterana 255
Apidae **206**, 207–54
  gen. et spp. indet. **254**
  incertae sedis 250–4
Apini 206, **225**, 226–49
Apis 177, 202, 213, 226–8, 230, 232, **239**, 240–2, **243**, 244–51 ; see *Synapis*
  acervorum 194
  adamitica 176–7, 186
  amalthea 216–7
  aquitaniensis **250–1**
  armbrusteri **244–6**, 247–8
    scharmanni **246**, 247
    scheeri 246, **247**
    scheuthlei 246, **247–8**, 249
      seemanni 248
      zeuneri 248
  bicornis 183
  catanensis **257**
    avolii 257
  centuncularis 182
  cucurbitina 188
  cuenoti 240
  dormitans 184, 241, **251**
  dorsata 237, 243, 247, 249
  florea 237, 245, 249
  helvola 166

  iridiae 243
  malvae 193
  manicata 178
  meliponoides 225, 227, 229, 231
  melisuga 201, **248–9**
  mellifera 225, 237, 241, 243–8, **249**; pl. 4, fig. 6
    indica 243
  mellifica 239, 243, 249
  oligocenica (*oligocaenica*) 240–2
  palmnickenensis 233
  quadricincta 163
  rufa 183
  styriaca **251**
  terrestris 209
  truncorum 180
  violacea 189
  sp. 247
Apoidea 161 et seqq.
  fossils erroneously classified as **202–3**, 257
  gen. et spp. *incertae sedis* **201–2**, 256–7
Armbruster, L. 158
auricle 158
Axestotrigona erythra 217
  togoensis 217

Baltic amber 159–60, 166, 168, 172–5, 200, 207–8, 214, 228–39, 252–7
Bauckhorn, H. 160
Bedford, R. 205
bees' nests 203, 256
Biareolina 165, 167, 170
  neglecta 165, 167
Blattidium beroldingianum 255
Bombini 157, 206, 209
Bombus 190, 201, **209**, 210–3, 226–7, 232, 237, 254
  abavus **210–1**, 212–3; pl. 2, fig. 2
  antiquus **252–3**
  carbonarius **252**, 254
  conservatus 255
  crassipes **209–10**
  florissantensis 201, **212**, 213
  grandaevus 201, 212, **253**
  jurinei 189–90
  lapidarius 213
  muscorum **252**
  proavus **212–3**
  pusillus **252**, 254
  terrestris 209
Bombusoides mengei **253**
Böttingen 160, 245
Burmese amber 160, 223
Burrow, Col. H. 161
Bursey, Mr 229

Calyptapis 201, 209, 212
  florissantensis 209, 212
Camoins 160
Catania 257
Celliforma **203**, 204–6
  bedfordi 204–5; pl. 1, figs 7, 8
  favosites **203**, 206
  germanica **204**
  nuda **204**
  septata 205; pl. 1, fig. 9; pl. 2, fig. 1
  spirifer **203–4**
  sp. indet. 205
Centris clavipes 221
  cornuta 176
Ceratina 166, **188**
  cucurbitina 188
  disrupta **188**
Ceratinini **188**
Cereste 240
Chalcobombus **206–7**, 208, 214, 227–8, 232
    group 206
  hirsutus **207**
  humilis 206–7, **208**
  martialis **208**
Chalicodoma 182–3
Chiavone 201
Clavicera 188
Cockerell, T. D. A. 159
cockroaches 255
Colletidae **161–2**, 255
copal 160, 217–21, 249
Corent 195–6
Crematogaster 219
Ctenoplectra 172
Ctenoplectrella **172**, 173
  dentata 172
  splendens **255**
  viridiceps 172, **173**
Ctenoplectrinae **172**, 173–4
Cyrtapis **163**
  anomalus **163**

Dasypoda 171, **175**
depstum 158, 230
Diandrena 170
Dianthidium **179**, 180
  curvatum 179
  tertiarum **180**
Dominica 257

East African copal 160
Electrapis 206, **225–7**, 228–39, 254; see
  Protobombus, Roussyana
  apoides 226, **227–9**, 237
  meliponoides 225, 227, **229–31**, 233, 237;
    pl. 3, figs 5, 6
  minuta **257**
  tornquisti **231**, 237
Eucera 178–9, 201, 212, 253
  antennata 193
  mortua 178–9, 193
Eucerini **192–3**
Euglossa 237
Euglossini 206

Florissant 161, 163 et seqq.
Formicinae **202**
Fraas, O. 158

Gabbro 201, 249
Gard 193
Glyptapis 172, **173**, 174
  fuscula **173**
  mirabilis **173–4**
  neglecta **174**
  reducta **174**
  reticula 174
  reticulata **174**

Halictidae **162**, 163–5
Halictinae **162–3**, 164–6
Halictoides maurus 170
Halictus **163**, 167–8, 171, 175, 198
  florissantellus **164**
  miocenicus **164**
  ruissatelensis **164**
  schemppi **164–5**
  scudderiellus **164**
Haplomelitta 174
Hauff, B. 159
Hauffapis 239, 243–4
  scharmanni 244, 246
  scheeri 244, 247
    gallauni 247
    rahdei 247
  scheuthlei 243–4, 247
    seemanni 247–8
    zeuneri 247–8
Heer, O. 161
Heriades **180**, 181–2
  bowditchi **181**
  halictinus **181**
  laminarum **181**, 182
  mersatus **181**
  mildredae **181–2**
  priscus **182**
  saxosus **182**
  truncorum 180
Hermann, P. 159
Hesperapis rhodoceratus 170
Hukong Valley 160, 223
Hylaeus albilabris 188
Hypotrigona **218**, 219–21
  bottegoi 218
  dominicana **256**
  eocenica **256**
  gribodoi **218–21**; pl. 2, figs 5–7

Klebs, R. 159
Krantz, F. 160
Krottensee 209

larval chambers 203–6, 256
Lerida 155
Lestrimelitta 206, 213, 217
Libellulapis **170**, 171
  antiquorum **170**
  wilmattae 170, **171**
Liotrigona bottegoi 218
Lithandrena 165, **169**
  antiquorum 169
  saxorum **169**
Lithanthidium **180**
  pertriste **180**
Lithoblatta lithophila **255**
Lithophaga nuda 204
Lithurge **176**, 177–8
  adamitica **176–8**
  cornutum 176
Lithurginae **176**, 177–8
Lithurgus 176–7
  adamiticus 177
Luke Thomas Collection 160

Macrocera 193
Mainz 159
Manning, Dr F. J., obituary 156
Megachile 179–80, **182**, 183
  amaguensis **182**
  centuncularis 182
  praedicta **183**
  sp. indet. **183**

Megachilidae 172, **175**, 176–87
  gen. et sp. indet. **186**
Megachilinae 176, **178**, 179–86
Megachilini **180**, 181–6
Megilla pilipes 194
Melectini 192, **199**
Melipona 213, 224, 254
  togoensis 217
Meliponini 206, **213**, 214–25
Meliponorytes 216, 223
  devictus 222–4
  sicula 216, 224
  succini 216–7, 221
Meliponula 217
  boccandei 217
Melissodes 212
Melitta **175**
  tricincta 175
  willardi **175**
Melittidae **171**, 172–5
Melittinae **174–5**
Menat 256
Mesoblattina lithophila 255
Mexico 257
Michener, C. D. 156, 161, 192
Musca lithophila 255

native bee 257
Naucoris carinata 255
Nogueirapis silacea **257**
Nomada 167
Nomia 169

Oeningen 159, 161, 177, 185–6, 190, 196–8, 201, 210
Orthoptera 255
Osmia 167, 180, **183**, 184–6, 202, 205
  antiqua 183, **184–5**
  bicornis 183
  carbonum **184**, 253
  dormitans 251
  sp. ? *dubia* 183, 185–7
  immortua 183, 186
  kirbyana 183, 202–3
  nigra 183, **185–6**; pl. 1, figs 5, 6
  primaeva 167, 183
  spp. indet. **186**, **256**

Panurginae **170**, 171
Panurgus 170
Parandrena andrenoides 170
Parschlug 251
Pelandrena 165, **169**, 170
  reducta 169, **170**
Perdita 170
Piski 202
Podalirius 194, 204
Polistes 203
  kirbyanus **202–3**
Probombus hirsutus **256**
Prohalictus 163
  schemppi 163–4
Protobombus 227, **231–2**, 233
  indecisus 231, **232–3**
  tristellus **233**
Protomelecta **199**
  brevipennis **199**

Radoboj 159, 195, 253
Randecker Maar 158, 164, 244, 246–8
Rohwer, S. A. 159
Ross, H. 157
Rott am Siebengebirge 157, 178, 184, 189, 200, 202, 240, 242–3, 251
Roussy, L. 160
Roussyana 227, **233**, 234–9
  palmnickenensis 226, **233–6**, 237, 254; pl. 3, figs 1, 2
  proava 228, **236–9**; pl. 3, figs 3, 4

Scheele Collection 160
Scheer, E. 159
Schempp, K. 159
Scheuthle, W. 158
Siberia 182
Sicilian amber 158, 224
Simjovel 257
Snodgrass, R. E. 156
Solnhofen 255
Sophrobombus 206, **213–4**, 215–6
  fatalis 213, **214–6**; pl. 2, figs 3, 4
South Australia 160
Sphecodes 164
Sphecoidea 155–6
Spokane 212
Statz, G. 160
Swinhoe, R. J. C. 160
Synapis 232, **240**, 241–3, 249
  cuenoti **240**, 241
  henshawi 237, **240–3**
    dormiens **241–2**, 251; pl. 4, figs 1–5
    kaschkei 240, **243**

Tetragona 216, **221**, 222–4
  elongata 221
  iridipennis **222–4** ; pl. 2, figs 8, 9
  succini **221–2**, 224
Tetragonula 222
Tetralonia **193**
  antennata 193
  berlandi 192, **193**
  duvaucelii 193
tibial comb, rake, spurs 157
Timon-David Collection 160
Tosi, A. 158
Trigona 214, **216–7**, 218–26, 236–7, 254 ; see *Hypotrigona*, *Nogueirapis*, *Tetragona*
  amalthea 216–7
  braunsi 218
  bottegoi 218, 220
  devictus 222
  dominicana 256
  elongata 221
  eocenica 256
  erythra **217–8**
    togoensis 217
  gribodoi 218
  iridipennis 222
  laeviceps 222–4
  sicula **224–5**
  togoensis 217–8
Trinidad 255

Uruguay 205–6
  auroranormai **205–6**

wasp 183, 202
  nest 203
Wheeler, Dr W. M. 159
Wickham, Professor H. F. 161
wing venation 157

Xilocopa 189
Xylocopa **189**, 190–2, 210–1
  abavus 210
  friesei **189**
  hydrobiae **189**
  jurinei **189–90**
  senilis 189, **190–2** ; pl. 1, figs 3, 4
  violacea 189
Xylocopinae **187–8**, 189–92
Xylocopini **188–9**, 190–2

Zeuner, Professor F. E., obituary 156

Professor F. E. Zeuner,
Ph.D., D.Sc., F.S.A., F.G.S., F.Z.S.†
F. J. Manning, Ph.D.†

S. F. Morris
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Accepted for publication 2 December 1975

PLATE 1

Anthophora melfordi Cockerell (p. 194)

Fig. 1. Holotype, BM(NH) I.9259. Oligocene, Florissant. × 2·5.

Andrena primaeva Cockerell (p. 167)

Fig. 2. Holotype, ETH Zürich SN.202. Miocene, Oeningen. × 5.

Xylocopa senilis Heer (p. 190)

Figs 3, 4. ETH Zürich 21. Miocene, Oeningen. × 2, × 2·2.

Osmia nigra sp. nov. (p. 185)

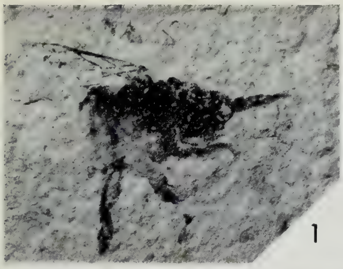
Fig. 5. Holotype, ETH Zürich Pl. I. 719. Head and thorax. Miocene, Oeningen. × 4·5.
Fig. 6. Holotype, ETH Zürich Pl. I. 719. Abdomen. Miocene, Oeningen. × 4·5.

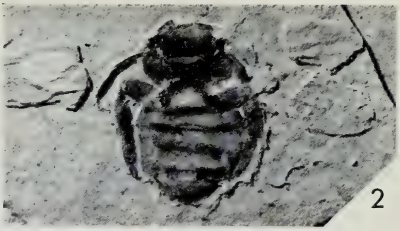
Celliforma bedfordi sp. nov. (p. 204)

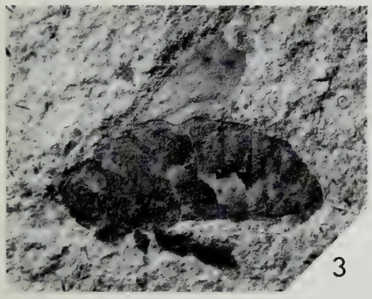
Fig. 7. Holotype, BM(NH) In.31434. Lateral view. Pleistocene or Sub-Recent, Venus Bay, South Australia. × 0·9.
Fig. 8. Holotype, interior view. Horizon and locality as Fig. 7. × 2·0.

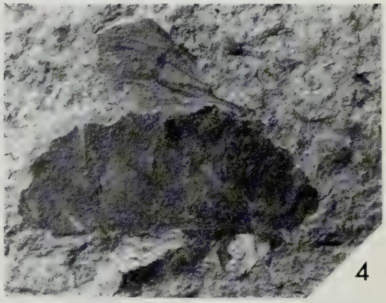
Celliforma septata sp. nov. (p. 205 ; see also Pl. 2, fig. 1)

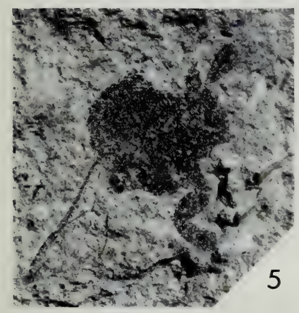
Fig. 9. Holotype, BM(NH) In.31433. Horizon and locality as Fig. 7. × 1.

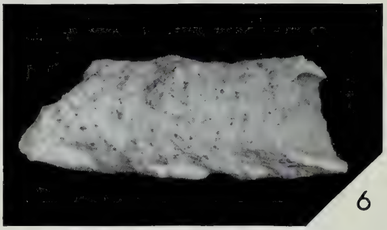

1

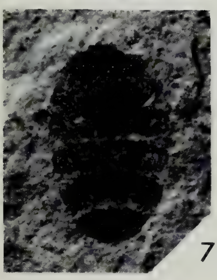

2

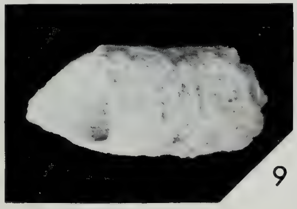

3


4


5


6


7


9

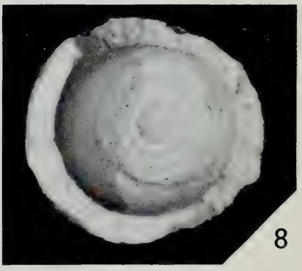

8

PLATE 2

Celliforma septata sp. nov. (p. 205 ; see also Pl. 1, fig. 9)

FIG. 1. Paratype, BM(NH) In.31435. Longitudinal section. Pleistocene or Sub-Recent, Venus Bay, South Australia. ×1.

Bombus abavus Heer (p. 210)

FIG. 2. ETH Zürich Pl. I. 808. Miocene, Oeningen. ×3·3.

Sophrobombus fatalis Cockerell (p. 214)

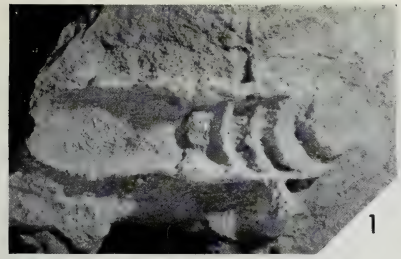
FIG. 3. Hamburg, Scheele Collection 1225. Eocene, Baltic amber. ×7·5.
FIG. 4. Hamburg, Scheele Collection 1225. Eocene, Baltic amber. ×8.

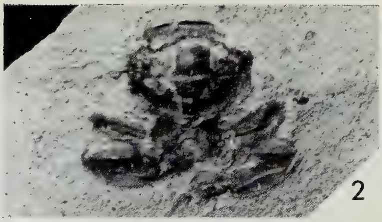
Trigona (Hypotrigona) gribodoi Magretti (p. 218)

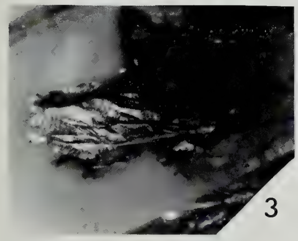
FIG. 5. BM(NH) In.38984. Pleistocene copal, East Africa. ×10.
FIG. 6. BM(NH) In.38984. Pleistocene copal, East Africa. ×12.
FIG. 7. BM(NH) 58511. Pleistocene copal, East Africa. ×10.

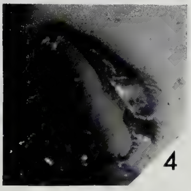
Trigona (Tetragona) iridipennis Smith (p. 222)

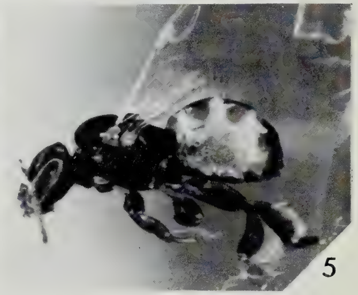
FIG. 8. BM(NH) In.43809. ? Pleistocene, Burmese amber, Hukong Valley, Burma. ×11.
FIG. 9. BM(NH) In.20702. ? Pleistocene, Burmese amber, Hukong Valley, Burma. ×13.

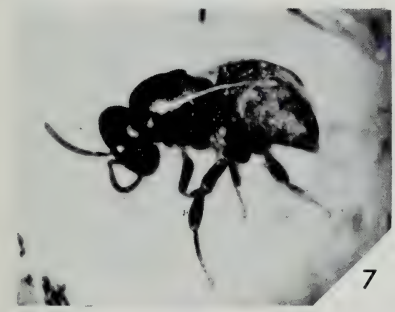

1

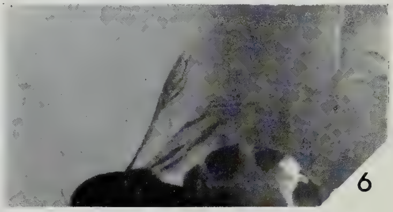

2

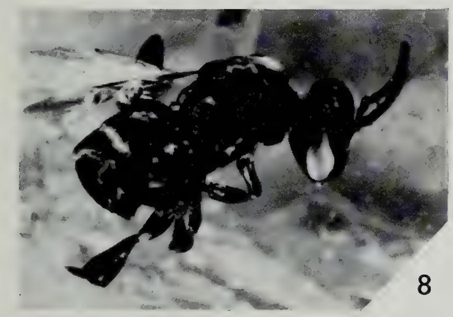

3


4


5


7


6


8

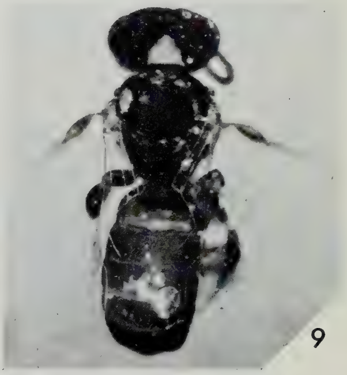

9

PLATE 3

Electrapis (Roussyana) palmickenensis (Roussy) (p. 233)

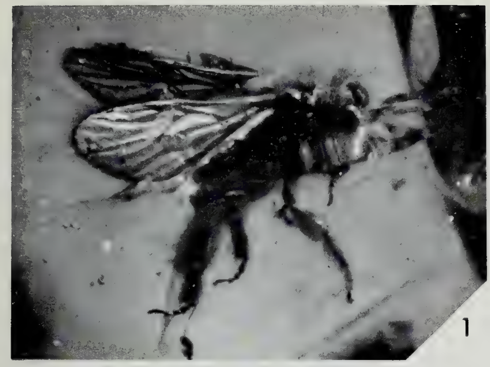
FIGS 1, 2. Hamburg, Scheele Collection 218. Eocene, Baltic amber. Fig. 1, ×11 ; Fig. 2, ×5·5.

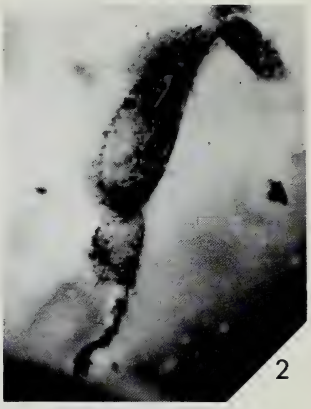
Electrapis (Roussyana) proava (Menge) (p. 236)

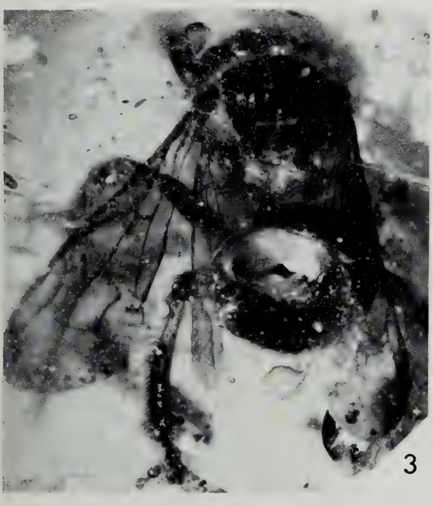
FIG. 3. Lectotype, BM(NH) In.43592. Eocene, Baltic amber. ×5.
FIG. 4. Paralectotype, BM(NH) In.18757. Eocene, Baltic amber. ×4·5.

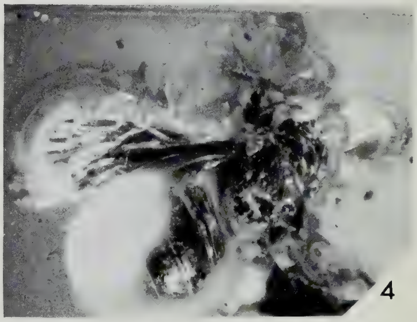
Electrapis (Electrapis) meliponoides (Buttel-Reepen) (p. 229)

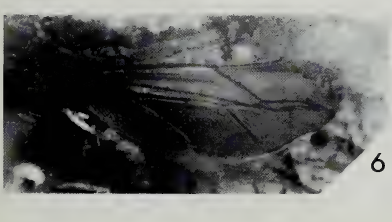
FIGS 5, 6. Hamburg, Scheele Collection 238. Eocene, Baltic amber. ×7·5.


1


2


3


4


6

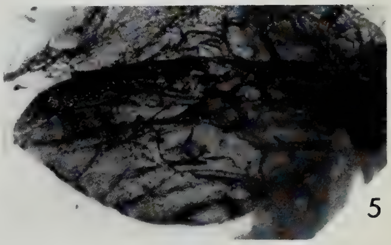

5

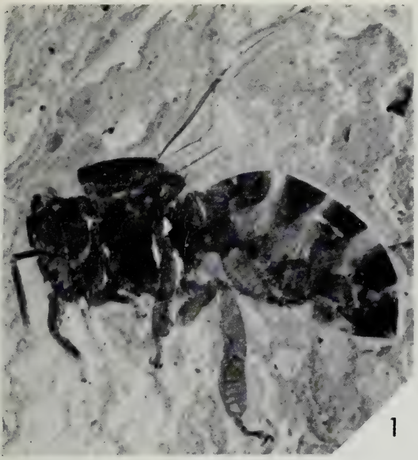
PLATE 4

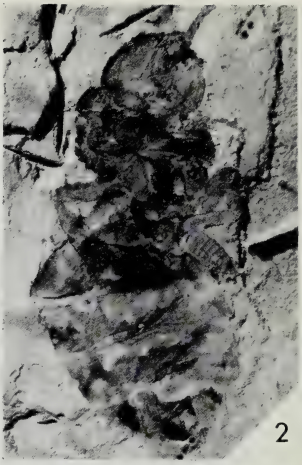
Apis (Synapis) henshawi dormiens subsp. nov. (p. 241)

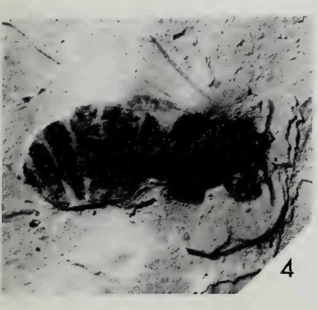
Fig. 1. Statz Collection. Oligocene, Rott. × 4.
Fig. 2. BM(NH) In.36655. Oligocene, Rott. × 5.
Fig. 3. Statz Collection. Oligocene, Rott. × 4.
Fig. 4. BM(NH) 59634. Oligocene, Rott. × 2·6.
Fig. 5. Statz Collection. Oligocene, Rott. × 4.

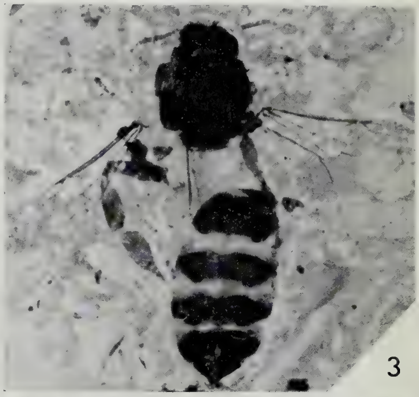
Apis (Apis) mellifera Linnaeus (p. 249)

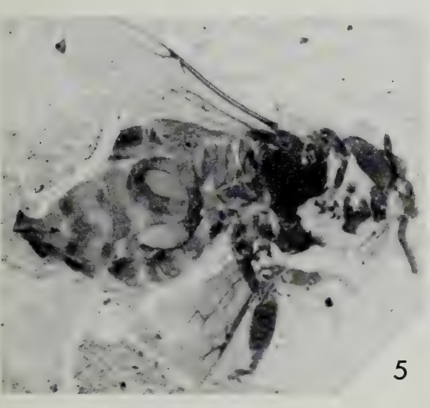
Fig. 6. BM(NH) 58576. Pleistocene copal, East Africa. × 4.

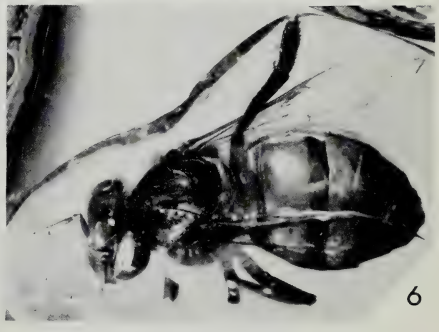

1


2


4


3


5


6

A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. Cox, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. OUT OF PRINT.
2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £11.
3. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £8.20.
3. Appendix. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.
4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 16 Text-figures. 1968. OUT OF PRINT.
5. Rhodes, F. H. T., Austin, R. L. & Druce, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 313; 31 Plates; 92 Text-figures. 1969. £13.10.
6. Childs, A. Upper Jurassic Rhynchonellid Brachiopods from Northwestern Europe. Pp. 119; 12 Plates; 40 Text-figures. 1969. £5.25.
7. Goody, P. C. The relationships of certain Upper Cretaceous Teleosts with special reference to the Myctophoids. Pp. 255; 102 Text-figures. 1969. £7.70.
8. Owen, H. G. Middle Albian Stratigraphy in the Anglo-Paris Basin. Pp. 164; 3 Plates; 52 Text-figures. 1971. £7.20.
9. Siddiqui, Q. A. Early Tertiary Ostracoda of the family Trachyleberididae from West Pakistan. Pp. 98; 42 Plates; 7 Text-figures. 1971. £9.60.
10. Forey, P. L. A revision of the elopiform fishes, fossil and Recent. Pp. 222; 92 Text-figures. 1973. £11.35.
11. Williams, A. Ordovician Brachiopoda from the Shelve District, Shropshire. Pp. 163; 28 Plates; 11 Text-figures; 110 Tables. 1974. £12.80.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

8BM.O

MUSEUM
GENERAL
27 OCT 1976
LIBRARY

MISCELLANEA

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 4
LONDON: 1976

BRITISH MUSEUM
GENERAL
27 OCT 1976
LIBRARY

MISCELLANEA

Pp 271–345 ; 12 *Plates* ; 12 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27, No. 4
LONDON: 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

These papers form Vol. 27, *No.* 4 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

© Trustees of the British Museum (Natural History), 1976

BRITISH MUSEUM (NATURAL HISTORY)

Issued 28 *October*, 1976

Price £7·95

CONTENTS

Page

Fusella M'Coy 1844, a problematic brachiopod genus from the Lower Carboniferous. By C. H. C. Brunton & A. Rissoné 275

The Jurassic Chaetetid, *Blastochaetetes bathonicus* J. C. Fischer, in England. By G. F. Elliott 285

Coprolites of *Ptilophyllum* cuticles from the Middle Jurassic of north Yorkshire. By C. R. Hill 289

A new fossil freshwater crab from the Ngorora Formation (Miocene) of Kenya. By S. F. Morris 295

Cyclothyris (Cretaceous Brachiopoda) from California. By E. F. Owen . 301

Cranial material of Oligocene and Miocene flamingos: with a description of a new species from Africa. By C. J. O. Harrison & C. A. Walker . 305

A new fossil pelican from Olduvai. By C. J. O. Harrison & C. A. Walker 315

Chelidonocephalus trilobite fauna from the Cambrian of Iran. By R. A. Fortey & A. W. A. Rushton 321

Index to Vol. 27 no. 4 341

FUSELLA M'COY 1844, A PROBLEMATIC BRACHIOPOD GENUS FROM THE LOWER CARBONIFEROUS

By C. H. C. BRUNTON & A. RISSONÉ

ABSTRACT

The genus *Fusella* is redescribed and assigned to the subfamily Strophopleurinae. Related or similar species are discussed.

INTRODUCTION

THE GENUS name *Fusella*, first published in 1844 by M'Coy for small transversely fusiform spiriferide brachiopods, has been poorly known and ill-used for about one hundred and thirty years. We redescribe the type specimen of the type species, *F. fusiformis* (Phillips), and other conspecific and congeneric material in the hope of establishing the genus *Fusella* on a more stable basis. Silicified specimens of *F. rhomboidea* (Phillips) allow the description of interiors believed to be closely comparable to those of *F. fusiformis*. The genus is formally redescribed and we discuss both its position within the Spiriferacea and those species which, in the past, have been assigned to *Fusella*.

SYSTEMATICS

Superfamily **SPIRIFERACEA** King 1846

Family **MUCROSPIRIFERIDAE** Pitrat 1965

Subfamily **STROPHOPLEURINAE** Carter 1974

DIAGNOSIS (emended). Small to medium very transverse Mucrospiriferidae with simple lateral costae and lirate, subimbricate micro-ornamentation. Fold and sulcus commonly non-costate, with or without median rib and groove; sulcus bounding ribs commonly accentuated, as are corresponding dorsal grooves. Ventral interarea large and denticulate. Dental plates short or buried by shell thickening. Dorsal sockets small and closely set; cardinal process commonly medially supported by short ridge; shell substance impunctuate.

DISCUSSION. Recently Carter (1974) proposed a classification of the Spiriferidae which involved the erection of the Strophopleurinae. Into this subfamily he placed '*Strophopleura* Stainbrook, 1947; *Alispirifer* Campbell, 1961; *Acuminothyris* Roberts, 1963; *Voiseyella* Roberts, 1964 (=*Amesopleura* Carter, 1967); ? *Eleutherokomma* Crickmay, 1950; ? *Pterospirifer* Dunbar, 1955; ? *Celsifornix*' Carter (1974 : 677). This subfamily corresponds partially with a new taxon of the authors' which was in script form at the time of Carter's 1974 publication. We accept

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 275–284

Issued 28 *October* 1976

Carter's subfamily but emend its taxonomic position and, importantly for the purpose of this paper, add the genus *Fusella* as a firm member of the subfamily. We believe that *Alispirifer* Campbell doubtfully belongs here but would suggest the inclusion of *Brachythyrina* Frederiks 1929 and *Paeckelmanella* Likharev 1934. Roberts (1971) placed *Voiseyella* in the Mucrospiriferidae but the above grouping within the Strophopleurinae removes *Fusella* and *Brachythyrina* from the Spiriferidae. *Alispirifer*, *Paeckelmanella* and *Pterospirifer* are removed from the Licharewiinae and *Eleutherokomma* from the Acrospiriferinae of the Treatise (Williams *et al.* 1965) classification.

Ivanova (1972 : 315) proposed the family Paeckelmanellidae for *Paeckelmanella*, *Alispirifer*, *Spiriferinaella* and *Pterospirifer*. The family was placed, with some reservation, in the Syringothyridacea, within the suborder Spiriferidina, but neither a full diagnosis nor a discussion was provided. Carter's subfamily, here used, partially equates with Ivanova's family, as can be seen from the generic constituents. Ivanova, Carter and we ourselves all agree that the taxon containing *Paeckelmanella* – and we believe *Fusella* – belongs within the Spiriferidina, but at family levels of classification there is no agreement ; Ivanova placed the mucrospiriferids within the new suborder Delthyrididina whereas most previous authors placed them in the Spiriferidina.

Genus ***FUSELLA*** M'Coy 1844

TYPE SPECIES. *Spirifera fusiformis* Phillips 1836 : 210 ; pl. 9, figs 10, 11. By original designation of M'Coy (1844 : 132).

DIAGNOSIS. Small (commonly less than 30 mm wide) strongly transverse shells with pointed extremities. High, variably concave, denticulate ventral interarea extending full width of shell. Lateral profile subcircular. Ventral sulcus bordered by pair of prominent ribs, dorsal fold variably developed. Lateral ribbing weak to moderately developed. Dental plates close together within sulcus, subparallel and with callosity filling apex of delthyrium in large specimens. Crural bases converge to valve floor posteriorly. Shell impunctate.

DISCUSSION. Although M'Coy (1844) was reasonably precise, for that date, in his description of *Fusella*, the name has been ill-used ever since. This is because there is only one well-known specimen of the type species *F. fusiformis* in existence and from this it is impossible to learn any detailed information about the internal morphology. It is this species which M'Coy specified as the type of his new 'subgenus' *Fusella*, characterized as follows.

> 'Shell elongate transversely, fusiform, cardinal area wide, much curved ; beaks incurved. This group would embrace these little *Spirifers* of the mountain limestone which have a perfectly fusiform outline, the depth being equal to the length, and the sides cylindrical ; the cardinal area is extremely wide in proportion to their size and is always hollowed or much curved, thus contrasting with the narrow, flat area of the typical *Spirifers* while the strongly incurved beaks distinguish them from the *Cyrtiae*. It would include the *S. bicarinata*, *S. rhomboides*, &c. &c.' (1844 : 132).

M'Coy's description stressed the incurved nature of the ventral umbo, which leads to the belief that he had not seen Phillips' actual specimen of *F. fusiformis* in which the ventral interarea is almost flat, only being concave medially, close to the umbo. The umbo projects beyond the hinge line by no more than 1·5 mm ; Waterhouse (1970 : 3) is in error in writing that the 'umbo extended 2·5 mm beyond the hinge', probably because he took his measurement from his published illustrations which are at almost twice the stated magnification. M'Coy's description may therefore have been influenced by specimens from the Cork area of Ireland best assigned to *F. rhomboidea* (Phillips). This suggestion is further supported by the size quoted by M'Coy for *F. fusiformis*, viz. 'length four lines, width one inch three lines, depth four lines[1]' (1844 : 132), a width which is somewhat greater than that of the type specimen of *F. fusiformis*.

A review of the confused use of the name *Fusella* was published by Waterhouse (1970). He redescribed the type specimen, from the Gilbertson Collection in the British Museum (Natural History), and compared it with various other species in an attempt to suggest its affinities. He concluded that *Unispirifer* Campbell 1957, with which *Fusella* has sometimes been synonymized, was distinctive and we agree with this view. Waterhouse thought that the shell substance of *F. fusiformis* was punctate, leading him to discard species such as *Spirifer rhomboidea* Phillips as being closely related, but to the conclusion that *Fusella* was 'probably related to members of the Syringothyrididae' (1970 : 6). Both optical and scanning electron-microscope studies of the type specimen and second undoubted specimen of *F. fusiformis* show that the shell is not endopunctate but quite normal for impunctate spiriferaceans (Pl. 1, figs 20, 21).

Thomas (1971) is one of the latest of several palaeontologists to say that it seemed inadvisable to use the generic name *Fusella* until the type specimen was adequately known from topotypic material. Had the name fallen from use this would be a sensible suggestion but in view of its continued appearance in the literature, commonly quite incorrectly, it is desirable to further Waterhouse's contention that it should become a well-known genus in its own right. Following the Russian lead when Ivanova (1960) placed *S. tornacensis* de Koninck within *Fusella* some palaeontologists, such as Carter (1967), have placed species in *Fusella* which differ widely from *F. fusiformis*. Within their concept the genus is relatively less wide, very much longer and has a strongly uniplicate anterior commissure. Carter (1971) described the genus *Mirifusella*, said to be 'most similar to *Fusella* M'Coy', but in fact differing considerably in outline and internal features. We have, therefore, a situation in which some palaeontologists advise the suppression of the name *Fusella* and others use this name, at times quite incorrectly. Because of this confusion it is desirable to correct the use of *Fusella* to the best of our ability, even if this is done without resort to additional genuine topotypic material. In the collections of the British Museum (Natural History) there exists one specimen clearly conspecific with the type specimen of *F. fusiformis*. This second specimen is in the Davidson Collection (B 7379) and came from Dovedale, Derbyshire (Pl. 1, figs 5–7). The ventral umbo has been broken from this specimen and it is possible to see that the dental plates did not extend anterodorsally to support completely the teeth and delthyrial margin near the hinge line. Unfortunately searches in the Derbyshire or Bolland and Clitheroe areas have failed to reveal additional specimens. The information on internal morphology of *Fusella* is, therefore, mainly based upon the silicified Fermanagh specimens collected by Brunton and assigned to *F. rhomboidea* (Phillips), a species believed to be closely related to *F. fusiformis* and which originally also came from Bolland (Pl. 1, figs 13–19).

---

[1] A line or ligne is one twelfth of an inch (=2·1167 mm).

In the last twelve years two genera have been proposed which are probably synonymous with each other and also are closely related to *Fusella*. These are *Voiseyella* Roberts 1964, with type species *Strophopleura anterosa* Campbell 1957 from the Lower Carboniferous of the Werria Basin, New South Wales, Australia, and *Amesopleura* Carter 1967, with type species *Spirifer novamexicana* Miller 1881 from the Lower Carboniferous (Osagian) of New Mexico. Both these authors thought that *Spirifer mundula* Rowley 1893 should probably be placed in their genus. Subsequently Roberts (1971) has placed *Amesopleura* into synonymy with *Voiseyella*. Having inspected Roberts' 1964 material from the Greenhills area of New South Wales and Carter's 1967 material from the Lake Valley region of New Mexico we agree with this synonymy. The question then arises as to the relationship of *Voiseyella* with *Fusella*. Neither Roberts nor Carter compared their genera with *Fusella*, although the former (1971) discussed the relationship of *Fusella* with *Unispirifer* and the latter placed his new species *llanoensis* (1967) within his concept of *Fusella*. These genera are clearly quite closely related ; their dimensions, outlines and profiles are very similar, as is the form of ribbing. The most important difference, and that which prevents the synonymy of *Voiseyella* within *Fusella*, is that the dental plates of *Voiseyella* diverge from the umbo following the ribs bordering the sulcus whilst those of *Fusella* are unusual in remaining subparallel within the confines of the ventral sulcus (Pl. 1, fig. 19) ; they do not follow the borders of the sulcus, as in many spiriferaceans. (The dental plates of *V. novamexicana* also follow the ribs bordering the ventral sulcus.)

In view of the varied use of the name *Fusella*, and despite the redescription by Waterhouse (1970), it seems desirable to provide a description of *F. fusiformis* based upon the type specimen and second specimen in the Davidson Collection.

Fusella fusiformis (Phillips)

Pl. 1, figs 5–12

1836 *Spirifera fusiformis* Phillips : 217 ; pl. 9, figs 10, 11.
1849 *Spirifera fusiformis* Phillips ; Brown : 108 ; pl. 51, figs 4, 5.
1858 *Spirifera fusiformis* Phillips ; Davidson : 56 ; pl. 13, figs 15, 15a.
1970 *Fusella fusiformis* (Phillips) ; Waterhouse : 3 ; figs 1A–F.

TYPE SPECIMEN. The single specimen described and figured by Phillips (1836) in the Gilbertson Collection, British Museum (Natural History), B 249, from Bolland, Yorkshire.

DIMENSIONS. Width (incomplete) 22·6 mm. Mid-point to ear of more complete side 13·8 mm. Length 8·2 mm. Thickness 8·2 mm. Angle of sulcus 33°. An estimate of the complete width of the shell is about 28 mm.

Diagnosis. Small transversely narrowly rhombic shells as long as thick and about three and a third times as wide as long. High ventral interarea with only slightly projecting umbo. Ribbing weakly developed and dorsal median fold prominent only anteriorly ; dorsal umbo medially sulcate. Dental plates short and subparallel, diverging anteriorly less than the angle of sulcus.

Description. The tip of the right side of the shell is missing and sediment obscures two thirds of the interarea. The external surface has been deeply exfoliated in patches, especially on the ventral valve. Elsewhere the shell is somewhat eroded and on only one small area in the ventral sulcus is primary shell preserved. Thus details of external ornamentation cannot be given, nor is it possible to count the number of ribs with certainty other than on the left half of the dorsal valve where there are ten or eleven simple costae. Within the more deeply exfoliated secondary fibrous shell of the ventral valve short radially arranged traces of mantle canals are visible. Growth lines are clearly seen, especially on the dorsal valve (about 4 per mm at the side of the fold) and indicate a fusiform shape throughout ontogeny ; they became more prominent anteriorly. The ventral interarea is vertically grooved by flexures in the secondary fibres (Pl. 1, figs 10, 21) which formed a delicate denticulation of the hinge line at the inner surface. (When covered by primary shell this feature would not be visible.) The ventral sulcus is prominent but the expected dorsal fold is virtually lacking although its position is marked by a pair of bordering ribs more prominent than the others. There is a dorsal median depression which becomes shallower and less well defined anteriorly from the umbo. The anterior commissure is uniplicate. No internal structures can be seen in the specimen although the exfoliation of the ventral umbo shows the secondary fibres to be bent along lines interpreted as the bases of the dental plates. If this is correct, it can be said that the dental plates are positioned on the borders of the ventral sulcus at a distance of 2 mm from the umbo but anteriorly remain subparallel and thus within the diverging sulcus. (This is the same as is seen in the Fermanagh silicified material assigned to *Fusella.*)

The second specimen, from Dovedale (B 7379, Pl. 1, figs 5–7), is smaller than the holotype and in that it too has lost its right tip and ventral umbo it is less well preserved (half width 11·3 mm, length *c.* 6·3 mm, thickness 6·1 mm). The dorsal fold is slightly developed anteriorly, resulting in a rather more prominent uniplication of the anterior commissure than in the holotype. The broken ventral umbo allows it to be seen that the dental plates are short for they did not reach anteriorly to the plane of fracture. It is impossible to measure the angle of divergence of the ventral sulcus but an estimate of the delthyrial angle, based on the remaining dorsal half of the interarea, is 30°. As in the holotype, the dorsal umbo is unusually shaped with a shallow V-shaped groove about 1 mm long terminating anteriorly on the pair of large ribs bordering the fold. Inspection of the visible surfaces shows that the shell structure of both specimens is fibrous with no sign of endopunctation.

Discussion. It is unfortunate that *F. fusiformis* is a rare species in rocks of low to mid Viséan age. If it were not for the second conspecific specimen from Dovedale we might have considered the type specimen to be a freak. Indeed it is possible that the presence of a reasonably developed dorsal fold is more characteristic; this feature is better developed on the Dovedale specimen and it is unusual for a uniplicate spiriferacean not to have a better developed fold. Growth lines show that even at a dorsal valve length of 2·5 mm the commissure was uniplicate. The amplitude of the uniplication is 3·0 mm on the type specimen and 3·2 mm on the Dovedale specimen. The growth lines also show that these shells grew with a fusiform shape virtually throughout their postembryonic ontogeny; a growth line about 1 mm from the dorsal umbo indicates that the valve width at that stage was 4 mm.

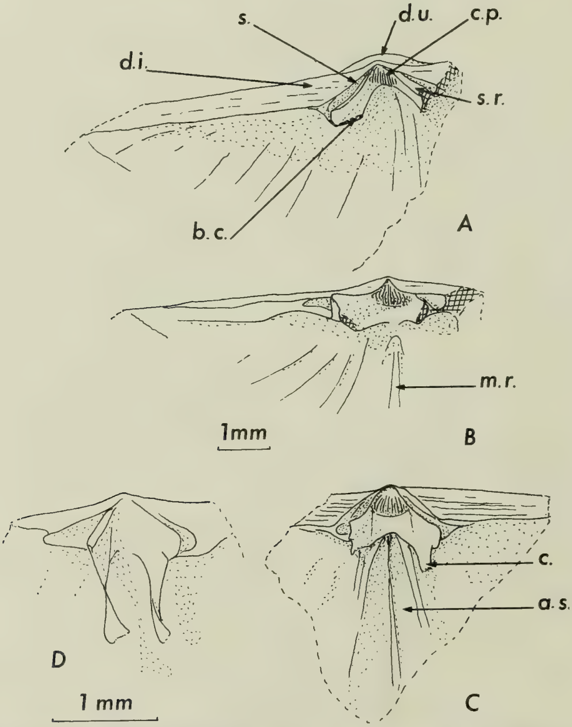


Fig. 1. Camera-lucida drawings of silicified dorsal valve interiors of *F. rhomboidea* (Phillips) from the Viséan of Co. Fermanagh, Ireland. A, B, dorsal and posterodorsal views of a nearly fully developed valve; C, dorsal view of part of a fully developed valve; D, dorsal view of a juvenile valve at twice the magnification. Note the posteriorly narrow sockets which, in adult shells, remained functional only anteriorly. Cross shading denotes broken shell material. a.s. – adductor muscle scar; b.c. – broken stump of the crus; c. – crus; c.p. – cardinal process; d.i. – dorsal interarea; d.u. – dorsal umbo; m.r. – median ridge (dividing the adductor scars); s. – socket; s.r. – socket ridge, which merges dorsally with the crural base. (See also Pl. 1, fig. 18.)

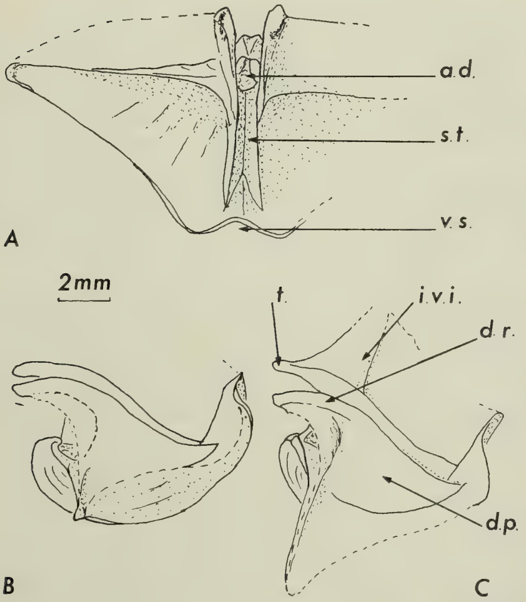


Fig. 2. Camera-lucida drawings of a silicified ventral valve of *F. rhomboidea* (Phillips) from the Viséan of Co. Fermanagh, Ireland. A, posterior view; B, lateral view; C, ventrolateral view. a.d. – apex of the delthyrium, filled by secondary shell material; d.p. – dental plate; d.r. – dental ridges bordering the interior surfaces of the edges of the delthyrium. Anteroventrally these ridges are supported by the dental plates which buttress across the ventral shell cavity. i.v.i. – internal surface of the ventral interarea; s.t. – secondary shell thickening between the dental plates; t. – tooth; v.s. – ventral sulcus. (See also Pl. 1, fig. 19.)

In the British Isles the species most closely resembling *F. fusiformis* is *F. rhomboidea* (Phillips), the type specimen of which also came from Bolland (Pl. 1, figs 13–17). This species is a constituent of the silicified brachiopod faunas being studied by Brunton (1966, 1968) from Ireland but as yet has not been redescribed except briefly by Brunton & Champion (1974). Other than *F. rhomboidea* there are several species mentioned by Waterhouse (1970), some of which he believed may belong to *Fusella*. It was his mistaken belief that *F. fusiformis* was endopunctate which led him to discard species like *rhomboidea*, *convoluta* (Phillips) and *trigonalis* (Martin) as being closely related. For the same reason Waterhouse related *Fusella* to *Syringothyris*, in particular some specimens believed to be *S. cuspidatus* (J. Sowerby). He figured (1970 : fig. 2, A–F) a specimen named '*Spirifer cuspidatus* (Phillips)' from Treak Cliff, Derbyshire, in the British Museum (Natural History) collections (BB 40831). This specimen belongs neither to the species *cuspidatus* (first described by Martin in 1809 but ascribed to J. Sowerby (1816) by Muir-Wood when she selected the lectotype in 1951) nor, since it is impunctate, to *Syringothyris* which includes only endopunctate species. The outline, even for a young specimen of *cuspidatus*, is too transverse, and furthermore true *cuspidatus* does not have a sulcate fold or denticulate ventral interarea such as that of the Treak Cliff specimen. Of the Gilbertson Collection specimens (B 297) from Bolland, labelled as *S. cuspidatus* and discussed by Waterhouse, only the largest three are true endopunctate *Syringothyris cuspidatus*. The fourth is poorly preserved and of doubtful affinity but the fifth is impunctate and like the Treak Cliff specimen BB 40831. These specimens should probably be assigned to the Strophopleurinae but do not accord with any presently described British species. Their dental plates are more like those of *Voiseyella* than *Fusella*.

Spirifer distans Sowerby is another species discussed by Waterhouse (1970) in the belief that it is closely related to *F. fusiformis*. Although some specimens assigned to *distans* may resemble *F. fusiformis* and despite true *S. distans* being impunctate, we do not believe it to be a *Fusella* species. The Sowerby type specimen of *S. distans*, from near Dublin, Ireland (B 61009), differs from *F. fusiformis* in external shape and a second Irish specimen (B 7664), more complete than the type refigured by Davidson (1858 : pl. 8, figs 5–8), is illustrated here for comparison (Pl. 1, figs 1–4). The dental plates of this species diverge, following the borders of the ventral sulcus, and there is an apically complete arched delthyrial plate.

Another species belonging in the subfamily but remaining difficult to assign to a genus, through a lack of internal information, is *Spirifer roemerianus* de Koninck, from the Tournaisian of Belgium. The same is true for the species *Spirifer triangularis* J. de C. Sowerby, placed in *Fusella* by Muir-Wood in 1951. This species is larger than *F. rhomboidea* and differs in having a high carinate fold and prominent ventral median rib in the sulcus. *Spirifer convoluta* Phillips is another extremely transverse species but it reaches much larger dimensions (at least 80 mm wide) than *F. fusiformis*. Its interior is unknown so the generic assignment is doubtful, but if it were to be included within *Fusella* the diagnosis of that genus would require emendation to include species at this size. *Spirifer bicarinata* M'Coy was one of the species M'Coy mentioned originally as being in *Fusella*. Other than by M'Coy's description and incomplete figure, *S. bicarinata* is virtually unknown ; the type specimen seems to be lost and it is unwise to continue using the name.

In conclusion, therefore, we assign *Fusella* to the Strophopleurinae and in addition to the type species, *F. fusiformis* (Phillips), we include *F. rhomboidea* (Phillips) and doubtfully *F. trigonalis* (Martin), *F. triangularis* (J. de C. Sowerby), *F. roemerianus* (de Koninck) and *F. convoluta* (Phillips) within this genus. *Strophopleura* probably evolved from the Mucrospiriferidae in the Upper Devonian and gave rise to the Tournaisian *Voiseyella* and *Acuminothyris* and to the Viséan *Fusella* ; from this the Carboniferous to Lower Permian genus *Brachythyrina* may have evolved, and also the northern Permian genera *Paeckelmanella* and *Pterospirifer*.

REFERENCES

Brown, T. 1849. *Illustrations of the fossil conchology of Great Britain and Ireland, with descriptions and localities of all the species.* viii + 273 pp., 117 pls. London.

Brunton, C. H. C. 1966. Silicified productoids from the Viséan of County Fermanagh. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **12** : 173–243, pls 1–19.

—— 1968. Silicified brachiopods from the Viséan of County Fermanagh (II). *Bull. Br. Mus. nat. Hist.* (Geol.), London, **16** : 1–70, pls 1–9.

—— & Champion, C. 1974. A Lower Carboniferous brachiopod fauna from the Manifold Valley, Staffordshire. *Palaeontology*, London, **17** (4) : 811–840, pls 107–111.

Carter, J. L. 1967. Mississippian brachiopods from the Chappel Limestone of central Texas. *Bull. Am. Paleont.*, Ithaca, **53** : 253–488, pls 13–45.

—— 1971. New early Mississippian silicified brachiopods from central Iowa. *Smithson. Contr. Paleobiol.*, Washington, **3** : 245–255, pls 1–2.

—— 1974. New genera of spiriferid and brachythyridid brachiopods. *J. Paleont.*, Tulsa, **48** (4) : 674–696, pls 1–4.

Davidson, T. 1858. A monograph of British Carboniferous brachiopods, **2** (5) 1. *Palaeontogr. Soc.* (*Monogr.*), London : 1–48, pls 1–8.

Ivanova, E. A. 1960. Spiriferida. *In* Orlov, Y. A. (ed.). *Principles of Palaeontology*, (**7**) *Bryozoa and Brachiopoda* : 264–280. Moscow (Akad. Nauk SSSR). [In Russian.]

—— 1972. Main features of Spiriferid evolution (Brachiopoda). *Paleont. J.*, Washington, **6** (3) : 309–320. [Translated from the Russian.]

M'Coy, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland.* 207 pp., 29 pls. Dublin.

Muir-Wood, H. M. 1951. The Brachiopoda of Martin's "Petrificata Derbiensia". *Ann. Mag. nat. Hist.*, London, (12) **4** : 97–118, pls 3–6.

Phillips, J. 1836. *Illustrations of the geology of Yorkshire. Part II. The Mountain Limestone district.* 253 pp., 25 pls. London.

Roberts, J. 1964. Lower Carboniferous brachiopods from Greenhills, New South Wales. *J. geol. Soc. Aust.*, Adelaide, **11** (2) : 173–194, pls 1–6.

—— 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, Northwestern Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Melbourne, **122** : 1–399, pls 1–59.

Thomas, G. A. 1971. Carboniferous and early Permian brachiopods from Western and Northern Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Melbourne, **56** : 1–272, pls 1–31.

Waterhouse, J. B. 1970. The Lower Carboniferous brachiopod genus *Fusella* M'Coy 1844. *Life Sci. Occ. Pap. R. Ont. Mus.*, Toronto, **15** : 1–12, pls 1, 2.

Williams, A. *et al.* 1965. Brachiopoda. *In* Moore, R. C. (ed.). *Treatise on Invertebrate Paleontology*, **H.** 927 pp., 746 figs. Kansas.

C. H. C. Brunton, Ph.D.
A. Rissoné
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Accepted for publication 9 February 1976

PLATE 1

The specimens are all housed in the BM(NH) and those in Figs 1–19 were coated with ammonium chloride sublimate before being photographed. The prints are not retouched.

Spirifer distans J. de C. Sowerby

Figs 1–4. Viséan of Millicent, Co. Kildare, Ireland. Viewed anteriorly, posteriorly, dorsally and from the left side. × 1. B 7664.

Fusella fusiformis (Phillips)

Figs 5–7. Viséan of Dovedale, Derbyshire. Viewed anteriorly, posteriorly and dorsally. The arrow on Fig. 7 indicates the region illustrated in Fig. 20. × 2. B 7379. Davidson Collection.

Figs 8–12. Holotype, figured by Phillips, from Bolland, Yorkshire. Viewed anteriorly, dorsally, posteriorly (the arrow indicates the region enlarged in Fig. 21), ventrally and from the left side. × 1·5. B 249. Gilbertson Collection.

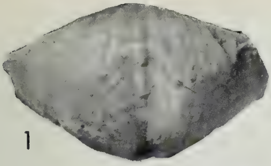
Fig. 20. Exfoliated standard secondary fibres from the position marked on Fig. 7. The posterior dorsal margin is to the top and the mid-line to the right. Scanning electron micrograph, × 210.

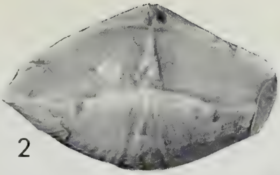
Fig. 21. Exfoliated secondary fibres of the ventral interarea of the holotype (see Fig. 10) showing the flexures resulting in a fine denticulation at the commissure. Scanning electron micrograph, × 140.

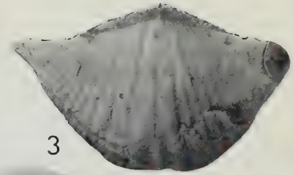
Fusella rhomboidea (Phillips)

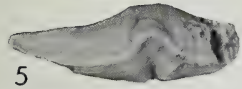
Figs 13–17. Lectotype, figured by Phillips, from Bolland, Yorkshire. Viewed ventrally, anteriorly, posteriorly, dorsally and from the right side. × 1; Figs 15, 17 × 2. B 236. Gilbertson Collection.

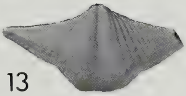
Figs 18–19. Silicified specimens from the Upper Viséan of the Sillees river, Co. Fermanagh, Ireland (see Brunton 1966 for locality details). Fig. 18, mature dorsal valve interior (see also Fig. 1A–D, p. 280), × 4. BB 61611. Fig. 19, young ventral valve interior looking posteriorly (see Fig. 2A–C, p. 281), × 3. BB 61612.

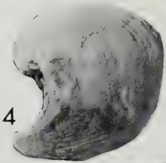

1

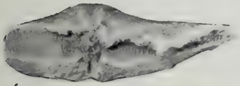

2

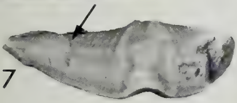

3

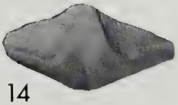

5

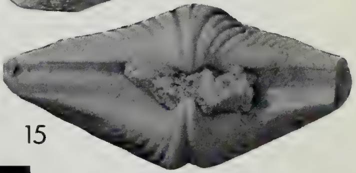

13

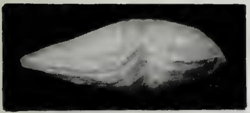

4

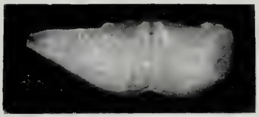

6

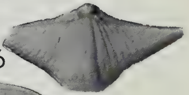

7

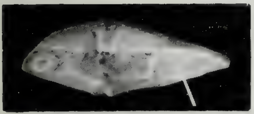

14

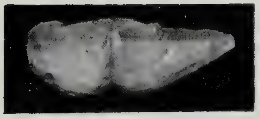

15

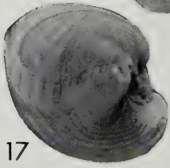

8

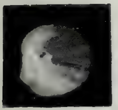

9

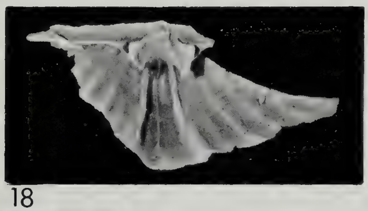

16

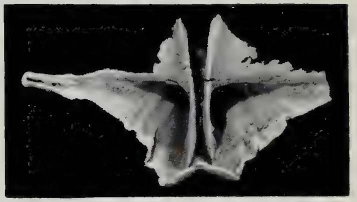

10

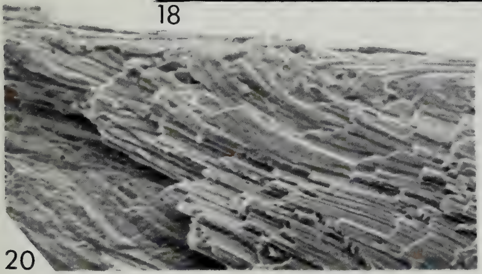

11

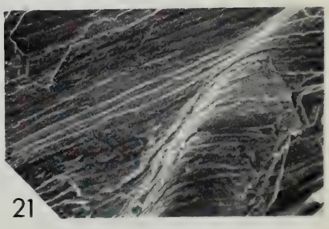

17


12


18


19


20


21

THE JURASSIC CHAETETID, *BLASTOCHAETETES BATHONICUS* J. C. FISCHER, IN ENGLAND

By GRAHAM FRANCIS ELLIOTT

ABSTRACT

Three English occurrences are listed of *Blastochaetetes bathonicus* Fischer, a species abundant in the French Bathonian east of the Paris Basin. It is suggested that their location, rarity and growth-forms may be due to migration, south of the Ardennes–London landmass, into less favourable conditions in the Cotswold area of southern England.

THE POST-PALAEOZOIC chaetetids were monographed by J. C. Fischer (1970). He discussed the structures and classification of these somewhat problematic calcified radial-tubular colonial organisms in detail, and compared them with bryozoa, tabulates and stromatoporoids, concluding that they were referable to the Hydrozoa (Coelenterata ; Cnidaria). His species *Blastochaetetes bathonicus* (Fischer 1965, 1970) occurs commonly in the Middle Bathonian of the Aisne and Ardennes in northern France, and is also recorded from Haute-Marne and the Côte-d'Or ; all these areas are in the Jurassic outcrop east of the Paris Basin. In Aisne and Ardennes the fossil is abundant in the 'Calcaires pseudo-oolithiques supérieurs', in which it forms characteristic banks or beds at some levels. Commonly it is accompanied by algal oncolites in a coarse-grained calcareous rock, suggesting that it flourished during life in agitated waters (Fischer 1969a, 1969b).

In England it appears to be a rare fossil, and only three occurrences are known to me, all Bathonian ; two are in Gloucestershire, and one near Bath (Elliott 1972, 1974). These records are now given in detail.

1. Great Oolite, probably near top of White Limestone. Tiltup's End, Nailsworth, Glos. For description of this old quarry, now overgrown, see Witchell (1886) and Woodward (1894 : 270). The specimen is in the British Museum (Natural History) Dept. of Palaeontology, registered number R 49314, Witchell Collection.
2. Great Oolite, probably near top of White Limestone. Limekiln Pit, Royal Agricultural College, Cirencester, Glos. Another old exposure (Woodward 1894 : 282). BM(NH) Dept. Palaeont. reg. no. R 49313, Hinde Collection (? *ex* Tomes Collection). Plate 2, figs 1–3.
3. Great Oolite, Upper Rags, Bed 3 of Elliott (1974). Bathampton Down, east of Bath, Avon (formerly Somerset). BM(NH) Dept. Palaeont. reg. no. R 49603, G. F. Elliott Collection. Plate 2, fig. 4.

In thin section all three specimens show the characteristic internal structures and approximate dimensions as given in full detail by Fischer (1970 : 179) ; the amber-coloured tube-walls with fibrous 'jet d'eau' or feather-structure are beautifully preserved. The external growth forms, however, are very different. The Tiltup's

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 285–288 *Issued* 28 *October* 1976

End specimen is a compact hemispherical growth exactly like that given as typical for the species by Fischer (1970 : fig. 20a, b), but is a small example (diameter 30 mm, as opposed to an average of 40 mm, maximum 120 mm, in the French material), No matrix remains. The Cirencester example is larger (approximate diameter 55 mm), higher-domed, and in section is seen to be grown round a coral nucleus of 15 mm diameter. It is interesting that this nucleus is almost completely altered to clear crystalline calcite, traces of identifying coral-structure surviving only at the margins, in contrast to the excellent preservation of the enveloping *Blastochaetetes*. The whole specimen is in a white pseudoolitic rock. Finally the Bathampton example occurs as thin irregular spreads, possibly crusts, of less than 10 mm thickness ; they are in an ochreous organic-rubble limestone with brachiopods, sponges, molluscs, echinoderms and bryozoa, whole and broken. The rock is interpreted as a current-accumulated deposit (Elliott 1974). This 'spreading' *Blastochaetetes* is regarded as a growth form only, for the Tiltup's End and Cirencester examples both contain old external surfaces heavily overgrown by later developments of the same organism.

The obvious and shortest migration-route in Bathonian times, from the colonies of the Aisne–Ardennes where the species flourished, was westwards in suitable facies south of the Ardennes–London landmass, and so to the clear-water calcareous site of the present Cotswolds in England. The areas to both north and south of this were in different facies. The species did not become abundant in England, and presumably did not survive into the changed conditions indicated by the overlying Forest Marble facies (Upper Bathonian). The recent 'Tentative reconstruction of the palaeogeography of part of southern England at the end of White Limestone times' (Palmer & Jenkins 1975 : fig. 6) indicates the Cotswold area as offshore-current marine. The numerous small facies-changes seen there in the actual rocks at about this level, as well as the rare varied growth forms of *B. bathonicus*, may well be evidence of less favourable conditions for the species than those which existed in France.

Note. Hartman & Goreau (1972), after a comparison with living Sclerospongiae, regarded the Chaetetida as extinct sclerosponges.

REFERENCES

ELLIOTT, G. F. 1972. *Cretacicrusta* gen. nov., a possible alga from the English Cretaceous. *Palaeontology*, London, **15** : 501–503, pls 100, 101.

—— 1974. Note on the palaeoecology of a Great Oolite fossil-bed at Bath (English Jurassic). *Proc. Geol. Ass.*, London, **85** : 43–48.

FISCHER, J. C. 1965. Découverte d'un niveau-repère à "Chaetetidae" dans le Bathonien moyen ardennais. *C. r. hebd. Séanc. Acad. Sci., Paris* **260** : 6641–6643.

—— 1969a. Géologie, paléontologie et paléoécologie du Bathonien au sud-ouest du Massif ardennais. *Mém. Mus. natn. Hist. nat. Paris* (n.s. C) **20**. 320 pp., 20 pls.

—— 1969b. Sur l'existence d'un cycle biostratigraphique dans le Bathonien au sud-ouest du Massif ardennais (Note préliminaire). *Bull. Soc. géol. Fr.*, Paris, (7) **10** : 303–307.

—— 1970. Revision et essai de classification des Chaetetidae (Cnidaria) post-Paléozoiques. *Annls Paléont.* (Invert.), Paris, **56** : 149–233, 6 pls.

HARTMAN, W. D. & GOREAU, T. F. 1972. *Ceratoporella* (Porifera: Sclerospongiae) and the Chaetetid "Corals". *Trans. Conn. Acad. Arts Sci.*, New Haven, **44** : 131–148, 26 figs.

PALMER, T. J. & JENKYNS, H. C. 1975. A carbonate island barrier from the Great Oolite (Middle Jurassic) of central England. *Sedimentology*, Oxford &c., **22** : 125–135.

WITCHELL, E. 1886. On the Forest Marble and Upper Beds of the Great Oolite, between Nailsworth and Wotton-under-Edge. *Proc. Cotteswold Nat. Fld Club*, Gloucester, **8** : 267–280, pls 4, 5.

WOODWARD, H. B. 1894. The Jurassic Rocks of Britain, IV. The Lower Oolitic rocks of England (Yorkshire excepted). *Mem. geol. Surv. U.K.*, London, 628 pp.

G. F. ELLIOTT, D.Sc., Ph.D., F.G.S., F.L.S.
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

Accepted for publication 9 February 1976

PLATE 2

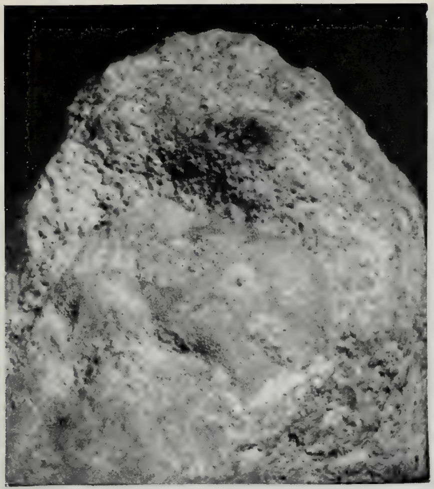
Blastochaetetes bathonicus J. C. Fischer

FIG. 1. Solid specimen, 'cauliflower-head' growth embedded in matrix, × 2. M. Jurassic, Great Oolite (Bathonian) ; Limekiln Pit, Royal Agricultural College, Cirencester, Glos. BM(NH) Dept. Palaeont., reg. no. R 49313.

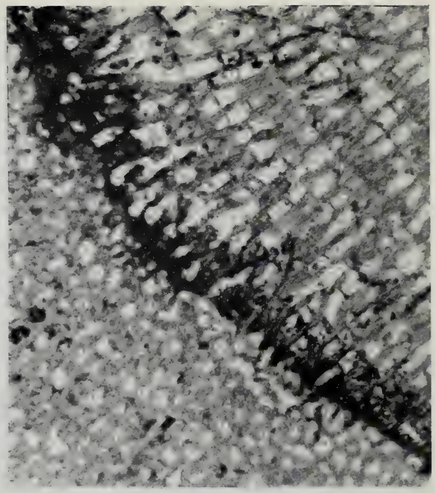
FIG. 2. The same specimen ; thin section, × 15, showing radial growth with old outer surface overgrown by a differently orientated second growth.

FIG. 3. The same specimen ; portion of outer surface, × 15.

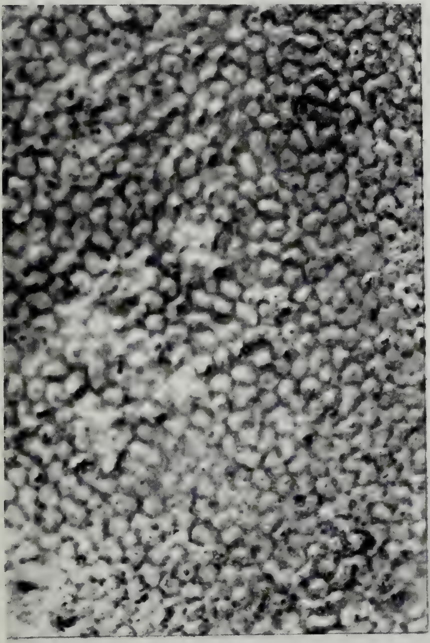
FIG. 4. Thin section of a spreading or laminar growth, × 15. M. Jurassic, Great Oolite (Bathonian) ; Bathampton Down, near Bath, Avon. BM(NH) Dept. Palaeont., reg. no. R 49603.



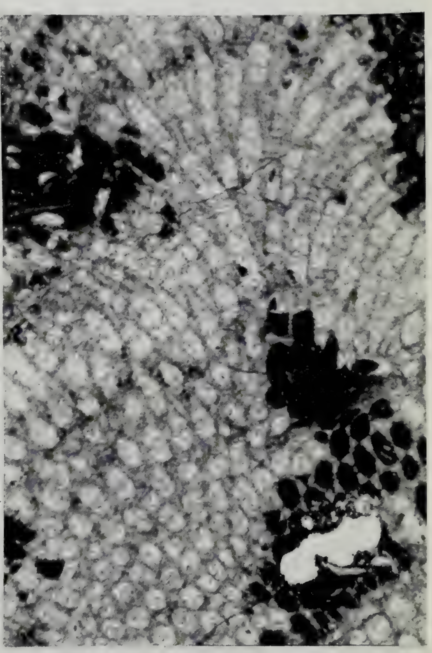
1



2



3



4

COPROLITES OF *PTILOPHYLLUM* CUTICLES FROM THE MIDDLE JURASSIC OF NORTH YORKSHIRE

By CHRISTOPHER RICHARD HILL

ABSTRACT

Large coprolites from the Roseberry Topping plant bed (Middle Jurassic) consist mainly of *Ptilophyllum* fragments. Their significance is discussed.

DESCRIPTION

THE SPECIMENS discussed here were collected over 50 years ago by Dr H. Hamshaw Thomas, though so far as I know he never described them. They were found in siltstones of Lower Deltaic age which form the upper layers of the Roseberry Topping plant bed (Thomas 1913). Besides being much the largest of the half dozen or so coprolites now known from the Yorkshire Middle Jurassic they have yielded an entirely different flora from those previously investigated.

The material is in the Collection of the Palaeontology Dept. of the British Museum (Natural History), and consists of six blocks labelled V 58510 and an additional one labelled V 58510a. Those labelled V 58510 look as if they once formed part of a single larger block which broke up in collecting, and judged on the six fragments this original block must have been large, having more than 250 pellets covering an area of about 1 m². As the pellets occur on several bedding planes, occupying about 5 mm thickness of the cross-bedded matrix, I assume that their burial was rapid. Otherwise I would expect them to have become widely dispersed, whereas they are in fact somewhat clustered into random groups, very like fresh droppings of a modern herbivore such as a rabbit. Indeed, much like freshly dropped rabbit pellets the round or oval outlines of the fossil ones sometimes show a constriction to a point on the side from which they were extruded, and fine striations, presumably caused by the anal sphincter, may be seen radiating from this point onto the impression surfaces. The clarity of these markings in the fossil doubtless indicates that the fresh pellets were of a firm consistency and also of a uniform, possibly gelatinous, texture.

The diameter of the pellets ranges from 8 to 18 mm, though they are mostly 10–13 mm. Where present the substance, which is composed of compressed cuticle fragments and finely divided organic detritus, is a dull black colour. It is about 0·5 mm thick, thinning to the edges, and the lack of compression border suggests that the pellets were perhaps somewhat flattened before their final burial (compression theory of Walton 1936). The fact that adjacent pellets sometimes overlap one another may equally indicate that they were originally rather flattened (Harris

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 289–294 *Issued* 28 *October* 1976

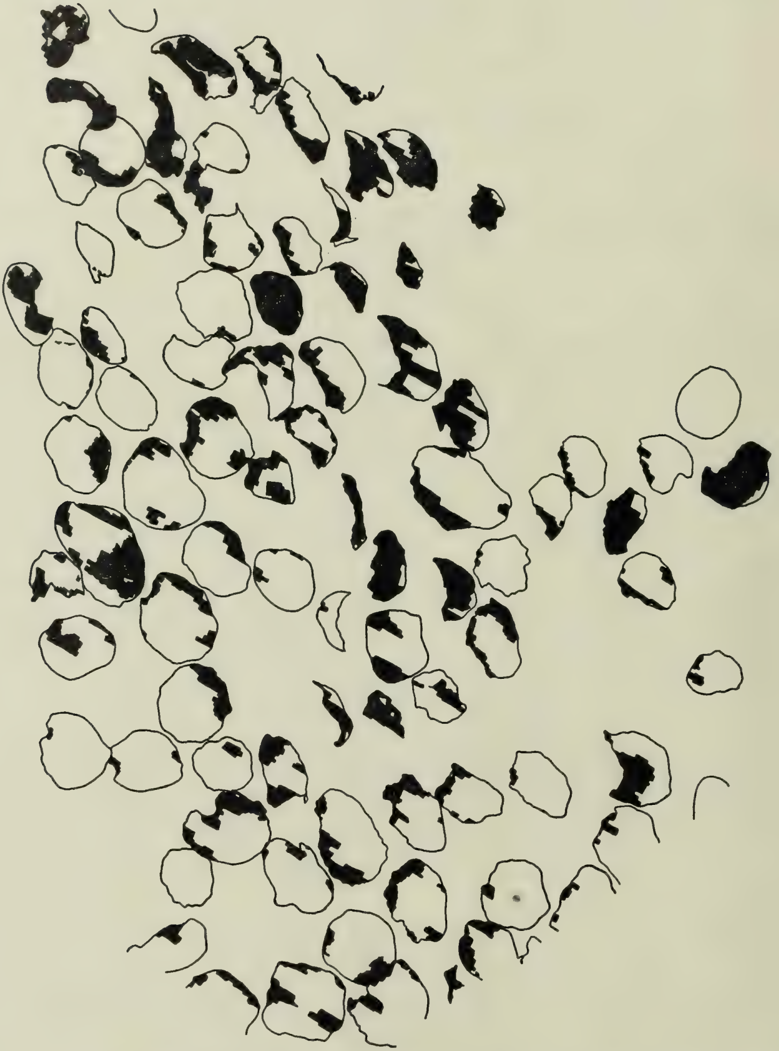


FIG. 3. Coprolite, chiefly of *Ptilophyllum pectinoides* (Phillips) Phillips, from Roseberry Topping, north Yorkshire. V 58510, × 1. Drawn on a photograph.

1946). However they could well overlap if, as in the pelleted form of sheep dung, they were sometimes produced adhering together in masses.

V 58510a may have come from a different horizon of the Roseberry Topping siltstone as the colour of the matrix is rather darker. The pellets have a similar form to those of V 58510 but they are uniformly smaller, about half the size, and many more of them overlap their neighbours. As, however, they yield an almost identical flora to those of V 58510 I imagine that they may well have been produced by the same kind of animal, but possibly an individual having a smaller anus ; by analogy a young rabbit produces much smaller pellets than a fully grown one.

Of the abundant cuticles yielded by Schulze-Ammonia maceration over 99% of the determinable ones are fragments from leaves and petioles of *Ptilophyllum pectinoides* (Phillips) Phillips. Only a few scraps from other species were seen, chiefly a specifically indeterminable *Solenites* or *Czekanowskia* and a Bennettitalean cuticle resembling *Nilssoniopteris vittata* (Brongn.) Florin (though possibly also referable to certain species of *Anomozamites* or *Pterophyllum*). There are in addition several well-preserved micropylar and interseminal scale cuticles identical with those of *Williamsonia hildae* Harris and *W. leckenbyi* Nathorst.

The size of the cuticle fragments reaches about 1 mm × 3 mm, though it is usually 1 mm^2 or smaller. The substance of the pellets, however, shows marked fracturing into rectangular blocks and this, which presumably occurred after deposition, may well have reduced the size of some of the cuticle fragments.

DISCUSSION

Coprolites from the Yorkshire Deltaic beds are rare and informative fossils. Other than occasional insects, fish skeletons and reptilian footprints they provide the only evidence so far known for the activity of vertebrate animals in the delta. The examples previously described, collected from the Gristhorpe Bed and at Beast Cliff, have been discussed by Harris (1946, 1951, 1956, 1964) and Harris *et al.* (1974). None of them, however, has pellets even as much as half the size of those in the present specimens and they have yielded entirely different floras, chiefly composed of comparatively delicate leaf and seed cuticles or pollen : mainly *Caytonia, Solenites, Androstrobus,* and thin Bennettitalean cuticles. In contrast to these the leaf of the Roseberry specimens, *Ptilophyllum pectinoides,* had a robust cuticle. Frequently also this leaf was resinous, as is indicated both in hand specimens and in the coprolite by the internal casts of mesophyll cells sometimes seen adhering in patches to the upper cuticle (Pl. 3, figs 1, 2, 3 ; Harris 1949). I conclude that the Roseberry herbivore was a rather larger animal than those which provided Harris's specimens, perhaps the size of a sheep or large rabbit. Indeed the present pellets are remarkably similar to the pelleted form of sheep's dung. The animal clearly could utilize the rather harsh resinous leaves of *Ptilophyllum,* though it did not digest the resin to any noticeable extent.

The nature of the herbivore is, of course, unknown, though presumably it was a reptile, such as an ornithopod dinosaur, or possibly a mammal. If a mammal then the pellets seem larger than would be expected from any mammals of Middle

Jurassic age so far described in the literature. Gut dimensions, however, though generally related to size, do not display a direct mathematical proportionality to it, and the analogy to the size of a sheep is approximate.

The intimate association, within the coprolite, of the flower *Williamsonia* with the leaf *Ptilophyllum* is striking. These organs are also seen associated together as hand specimens in the normal flora at Roseberry and on this basis, with additional evidence from morphologically intermediate organs, Harris (1969) has attributed them to the same plant. In this respect it seems that the coprolite provides a remarkably faithful representation of the normal Roseberry flora. Assuming that the animal fed on living plants the evidence thus reinforces Harris's restoration.

The overall floristic composition of the dung is also like that of the normal flora at certain layers in the upper part of the siltstone, and this is interesting in view of the complex factors, such as fragmentation and sorting, which normally operate during the deposition, as at Roseberry, of terrestrial plants in stream channel deposits. As it is natural to assume that the herbivore fed on living vegetation the facts suggest that the fragmentary debris which constitutes the normal fossil flora might sometimes be a remarkably straightforward representation of plant communities then growing in the vicinity. They may also indicate that the plants grew fairly close to Roseberry, for if the animal had strayed far one might expect the dung to yield at least a few species not normally found there.

There is, however, a simpler explanation. The animal may possibly have been a scavenger, browsing on the *Ptilophyllum* debris which was being transported in the deltaic streams and ultimately deposited in great abundance at Roseberry and other localities. If this is right the dung would be expected to show fragments of species we already know from the normal Roseberry flora, but it would not necessarily indicate anything about plant communities in the living vegetation other than that their debris could be palatable to an unknown animal.

Unfortunately there is insufficient evidence to make a certain choice between these explanations, though so far as I know there are no modern vertebrates which would normally prefer a diet of rotting leaves to fresh ones. For this reason the first explanation seems perhaps nearer the truth.

REFERENCES

Harris, T. M. 1946. Notes on the Jurassic Flora of Yorkshire, 19–21. *Ann. Mag. nat. Hist.*, London, (11) **12** : 357–378.

—— 1949. Notes on the Jurassic Flora of Yorkshire, 43–45. *Ann. Mag. nat. Hist.*, London, (12) **2** : 561–585.

—— 1951. Notes on the Jurassic Flora of Yorkshire, 49–51. *Ann. Mag. nat. Hist.*, London, (12) **4** : 915–937.

—— 1956. The investigation of a fossil plant. *Proc. R. Instn Gt Br.*, London, **36** (163) : 1–11.

—— 1964. *The Yorkshire Jurassic Flora*, **2** : *Caytoniales, Cycadales and Pteridosperms.* viii + 191 pp., 7 pls. Brit. Mus. (Nat. Hist.), London.

—— 1969. *The Yorkshire Jurassic Flora*, **3** : *Bennettitales.* vi + 186 pp., 7 pls. Brit. Mus. (Nat. Hist.), London.

—— Millington, W. & Miller, J. 1974. *The Yorkshire Jurassic Flora*, **4** : *Ginkgoales and Czekanowskiales.* viii + 150 pp., 8 pls. Brit. Mus. (Nat. Hist.), London.

THOMAS, H. H. 1913. The Jurassic plant beds of Roseberry Topping. *Naturalist*, London, **1913** : 198–200.

WALTON, J. 1936. On the factors which influence the external form of fossil plants ; with descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. *Phil. Trans. R. Soc.*, London, (B) **226** (535) : 219–237.

C. R. HILL, B.Sc., Ph.D.
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

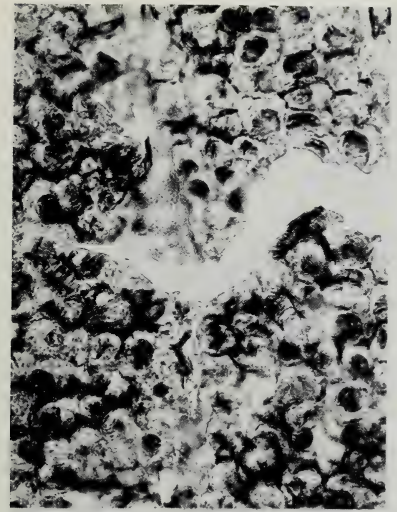
Accepted for publication 9 February 1976

PLATE 3

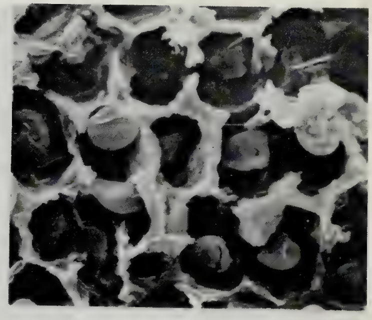
Ptilophyllum pectinoides (Phillips) Phillips

Figs 1, 2, 3. Upper cuticle prepared by Schulze maceration of a hand specimen found at Hasty Bank. Fig. 1, V 58591, light micrograph, × 160. Fig. 2, inner surface of cuticle; scanning electron micrograph showing resinous casts inside the 'cutinized' walls of palisade mesophyll cells, × 336. Fig. 3, same, × 1040.

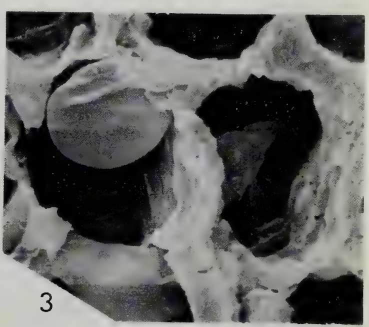
Fig. 4. Coprolite, chiefly of *Ptilophyllum pectinoides*, from Roseberry Topping. V 58510, × 1. Photo: J. V. Brown.



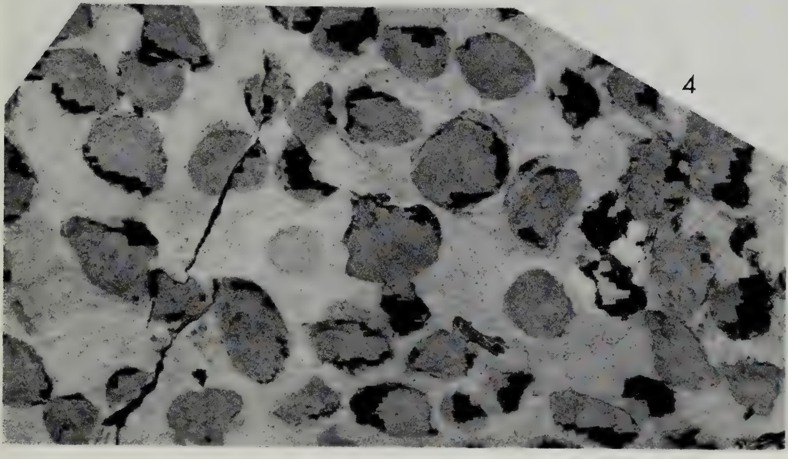
1



2



3



4

A NEW FOSSIL FRESHWATER CRAB FROM THE NGORORA FORMATION (MIOCENE) OF KENYA

By SAMUEL FRANCIS MORRIS

ABSTRACT

A new species of freshwater crab, *Potamonautes* (*Lirrangopotamonautes*) *tugenensis*, is described from the Miocene of the Tugen Hills, Kenya. It is compared with Recent species of *P.* (*Orthopotamonautes*) and *P.* (*Lirrangopotamonautes*).

MATERIAL

Dr Martin Pickford of Bedford College, London, whilst collecting fossil mammals from the Lake Baringo area of northern Kenya, collected a number of claystone nodules from the northern end of the Tugen Hills, about 20 miles (32 km) north-west of Lake Baringo. They came from the two neighbouring localities of Kamwina, Kabarsero area (Pickford locality 2/72) and Kalimale area (Pickford locality 2/68). The Kamwina locality is a lake shoreline deposit with diatomaceous shales and the Kalimale section is a relict river channel. Kamwina is Member C and Kalimale Member D of the Ngorora Formation of Miocene age, approximately $11\text{–}12 \times 10^6$ years (Bishop & Chapman 1970, Bishop, Chapman, Hill & Miller 1971). The Kalimale locality has yielded only isolated limb segments. For the latest assessment of the chronostratigraphy of the region, Berggren & van Couvering (1974) should be consulted.

The nodules collected by Dr Pickford contain freshwater crabs and ostracods. The brittle nodules are not laminated in any way so that attempts to break them open by hammer resulted in the shattering of the nodule. An attempt to develop the nodules by acid treatment was unsuccessful. It remained to split each one with a rock splitter, which was less damaging than the hammer but nevertheless reduced it to a number of fragments that had to be glued back together. If there was any preferred plane of splitting it was through the abdomen and along the smoother subhepatic and pterygostomial areas. Even though the specimens are in nodules they are crushed. Fortunately Dr Pickford had collected one specimen, the holotype, which had weathered free of matrix and was not badly crushed, and also some isolated segments of limbs. Altogether about 50 nodules were collected that contained crab remains. The limb fragments from Kalimale are not sufficiently different to suggest that a second species is present, but limb fragments are not very diagnostic. A modern freshwater crab species would probably not occupy both such diverse habitats as river channels and lake shores, since this would involve different water speeds, temperature and bottom conditions. Hence it is possible

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 295–300 *Issued* 28 *October* 1976

that a second species is present, but that problem can only be resolved by more and better material from Kalimale.

SYSTEMATICS

Section BRACHYRHYNCHA Borradaile 1907

Superfamily **XANTHOIDEA** Dana 1851

Family **POTAMIDAE** Ortmann 1896

Genus ***POTAMONAUTES*** Macleay 1838

Type species. *Thelphusa perlata* H. Milne-Edwards 1837, by subsequent designation of Rathbun 1905 : 159.

Subgenus ***LIRRANGOPOTAMONAUTES*** Bott 1955

Type species. *Potamon* (*Potamonautes*) *lirrangensis* Rathbun 1904, by original designation of Bott 1955 : 264.

Potamonautes (Lirrangopotamonautes) tugenensis sp. nov.

Pl. 4, figs 1–6

Diagnosis. A *Lirrangopotamonautes* with strongly produced front and medially divided urogastric area, single spines on the carpus and on the otherwise smooth merus.

Material. One more or less complete carapace, 50 distorted and fragmentary carapaces and some isolated chelipeds. The holotype and most of the paratypes are in the National Museum of Kenya, Nairobi. The remaining paratypes (nos In 61517–24) are in the British Museum (Natural History), London. The material comes from two Miocene localities in the Ngorora Formation, at Kamwina and Kalimale about 20 miles (32 km) NW of Lake Baringo, Tugen Hills, Kenya.

Description. Carapace one quarter wider than long at its widest point about one third back. The front is moderately long and strongly produced with only a slight ventral deflection ; it is smooth and occupies about one third of the anterior carapace width. The anterior margin is smooth and strongly sinuous with a thickened edge. On the holotype one ocular peduncle is preserved. The postfrontal crest is strong, overhangs the front and is nearly straight with a slight deflection towards the front at the mid-line ; it meets the anterolateral margin at an obtuse angle. The postfrontal crest and anterolateral margins are smooth or slightly beaded. The margins of the orbits are entire, thickened and smooth. The single extraorbital spine is well developed. The median furrows join at or only just posterior to the postfrontal crest and pass forward on to the frontal area, cutting the frontal area into two. The lateral margins are convex anteriorly and may be slightly concave posteriorly.

The anterolateral marginal ridge passes up on to the dorsal carapace just behind the widest part of the carapace. The posterolateral marginal ridge starts below the point at which the anterolateral marginal passes on to the dorsal carapace, and goes in an anteroventral direction.

The hepatic areas are inflated and traversed by two rows of pits. The line of the pits curves proximally across the branchial area to join the cervical groove opposite the widest part of the mesogastric area. The urogastric area is clearly delimited by the cervical groove and the furrow between the uro- and metagastric areas. The urogastric area is divided by a longitudinal furrow. The proximal walls of the cervical groove are deeply hachured on the internal mould (and probably also on the shell itself). The cervical groove is deep medially but becomes shallower anterolaterally. The rhomboidal branchial areas are inflated and covered with feeble rugosities.

The ventral surface is poorly preserved – usually only the first four thoracic sternites or hemisternites are preserved. No abdomina have been found except for one poorly preserved female, of which the segments appear simple and not fused. The third maxilliped is reasonably well preserved although no merus has yet been found. The ischium is broad and subrectangular ; it bears a groove parallel to the inner margin and about one third in. The exopodite is about a third of the width of the ischium and tapers anteriorly. The posterior inner angles of the ischia close against a knob-like anterior extension of the first thoracic sternite, which has the shape of a 'parson's nose'[1]. The lateral flanges of the anterior extension have two small swellings, sometimes extended into ridges, one on each flange. Although corresponding depressions have not been found on the underside of the ischia, they appear to have a press-stud effect presumably to locate accurately the third maxilliped when it is closed. The fingers of the larger, right, cheliped are approximately the same length as the palm and are gently curved towards the mid-line. The fingers are grooved laterally and bear large teeth. There is virtually no gape between the fingers, which are opposed throughout their length. The smaller cheliped is similar to the larger one except that the palm is narrower and the teeth of the fingers fine with an occasional larger tooth. The smooth carpus bears a single spine at the distal end of the inner marginal ridge. The ridge is sharp and strongly elevated. The merus also bears a single spine at the distal end of its inner marginal ridge but the outer marginal ridge is strong and smooth or may possibly have a few coarse granules.

DISCUSSION

Very few species of freshwater crabs have been found fossil and this is the first that can be assigned to a Recent genus. The form of the postfrontal crest and the shape and position of the epibranchial angle clearly indicate that it belongs to the Recent African genus *Potamonautes*. *Potamonautes* was split by Bott (1955) into fifteen subgenera, to a large extent on the form of the gonopods. However there are sufficient carapace differences to allow the fossils to be compared with the two subgenera *Lirrangopotamonautes* and *Orthopotamonautes*. Bott (1955 : 310) erected four new genera for fossil species of potamid crabs, but stated that on the characters of the carapace, which alone is usually preserved, the fossil species could be compared with Recent species. The closest species to the present fossils are the living *P.* (*Orthopotamonautes*) *depressus* (Krauss) and *P.* (*Lirrangopotamonautes*) *lirrangensis* (Rathbun). Both these are restricted geographically to central and east Africa at the present time. *O. depressus* has a weakly produced or even deflected front whereas *L. lirrangensis* has a strongly produced front similar to *L. tugenensis*. However *L. lirrangensis* has a denticulated anterolateral border and three rows of denticles on the merus of the cheliped. The widest part of the carapace of *O. depressus* lies just in front of the anterior third, whilst that of *L. tugenensis* lies just behind.

---

[1] Pygostyle of domestic fowl.

The many species of *Potamonautes* are distributed through central and southern Africa, especially in the tropical belts and the Rift Valley system. The majority have discontinuous distributions at the present day in the cooler water of the montane regions where they are found in many habitats from rapid-flowing rivers to shallow trickles or even standing water (Williams 1968). But some species groups, e.g. the *O. johnstoni* group (Williams 1968) to which *L. tugenensis* probably belongs, prefer the slow-moving warmer waters of the lakes and especially the coastal belts. The Kamwina fossils appear to come from lacustrine deposits in which the water could have been warm and slow-moving. The discontinuous occurrences of the Recent species appear to reflect a residuum of previous land forms. The single fossil species does not allow any reconstruction of previous drainage patterns, but a number of occurrences might give some clue both to the evolution of the drainage pattern and to the interrelationship of the many species of freshwater crabs from east Africa. Dr Keith Bannister is at present trying to unravel the drainage pattern of east Africa by studying the interrelationships of various species of the large fish *Barbus* which are also distributed through many separated bodies of water (personal communication).

Although *L. tugenensis* is the first fossil freshwater crab from Africa that can be assigned with any certainty to a modern genus, Joleaud & Hsu (1935 : 108 ; fig. 11) published a specimen, described as 'Potamonidé gen. nov.', from Cenomanian terrestrial deposits of Tanout, Niger (Furon 1935 : 35), which is difficult to assess from the outline figure. Unfortunately the figured specimen cannot be found at present in Paris. In the form of the postfrontal crest it could certainly belong to the Potamidae near *Potamonautes* but the two lateral crests do not conform to any Recent genus.

REFERENCES

Berggren, W. A. & van Couvering, J. A. 1974. The Late Neogene: Biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **16** : 1–216.

Bishop, W. W. & Chapman, G. R. 1970. Early Pliocene sediments and fossils from the northern Kenya Rift Valley. *Nature, Lond.* **226** : 914–918.

—— ——, Hill, A. & Miller, J. A. 1971. Succession of Cainozoic vertebrate assemblages from the northern Kenya Rift Valley. *Nature, Lond.* **228** : 389–394.

Borradaile, L. A. 1907. On the classification of the Decapoda. *Ann. Mag. nat. Hist.*, London, (7) **19** : 457–486.

BOTT, R. 1955. Die Süsswasserkrabben von Afrika und ihre Stammesgeschichte. *Annls Mus. r. Congo Belge*, Terverun, C. Zoologie (III, III) **1** (3) : 209–352, 30 pls, 103 figs.

DANA, J. D. 1851. On the Classification of the Cancroidea. *Am. J. Sci.*, New Haven, (2) **12** : 121–131.

FURON, R. 1935. Le Cretacé et le Tertiaire du Sahara soudonais. *Archs Mus. natn. Hist. nat. Paris* (6) **13** : 1–96, pls 1–7.

JOLEAUD, L. & HSU T.-Y. 1935. Crustacés décapodes du Cretacé de Tanout (Damergou Niger français). *Archs Mus. natn. Hist. nat. Paris* (6) **13** : 99–110, 11 figs.

MACLEAY, W. S. 1838. *Illustrations of the Zoology of South Africa* ; *Annulosa.* 75 pp., 4 pls. London.

MILNE-EDWARDS, H. 1837. *Histoire Naturelle des Crustacés* **2**. 532 pp. Paris.

ORTMANN, A. E. 1896. Das System der Decapoden-Krebse. *Zool. Jb.*, Jena, **9** : 409–453.

RATHBUN, M. J. 1904–5. Les Crabes d'Eau douce. *Archs Mus. natn. Hist. nat. Paris* (4) **6** : 224–312 ; **7** : 159–321 ; 18 pls.

WILLIAMS, T. R. 1968. The taxonomy of the East African River-Crabs and their association with the *Simulium neavei* complex. *Trans. R. Soc. trop. Med. Hyg.*, London, **62** : 29–34.

S. F. MORRIS
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

Accepted for publication 9 February 1976

PLATE 4

Potamonautes (Lirrangopotamonautes) tugenensis sp. nov.

Member C, Ngorora Formation, Miocene ; Kamwina, Kenya

FIG. 1. Holotype, Kenya National Museum. Dorsal carapace. × 1·5.

FIG. 3. Paratype, Kenya National Museum. Sternum and ischium. × 3.

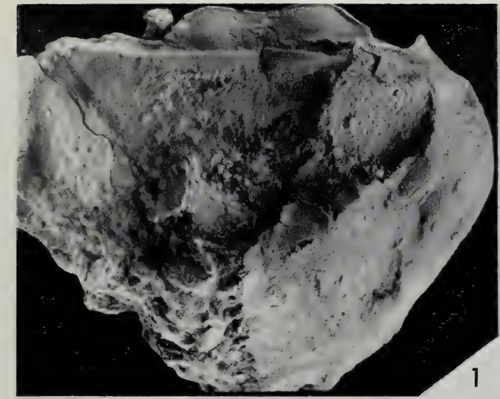
FIG. 4. Paratype, Kenya National Museum. × 1·2.

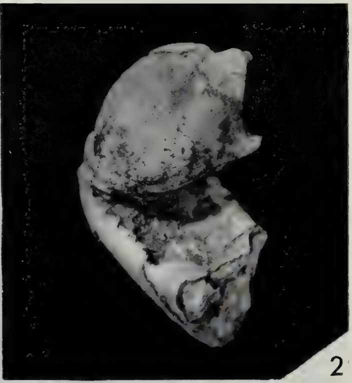
FIG. 5. Paratype, Kenya National Museum. Mesogastric and urogastric areas. × 3.

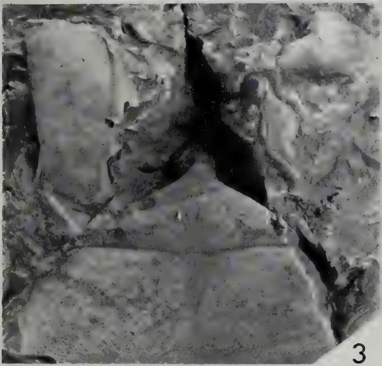
FIG. 6. Paratype, Kenya National Museum. Sternal 'knob'. × 3.

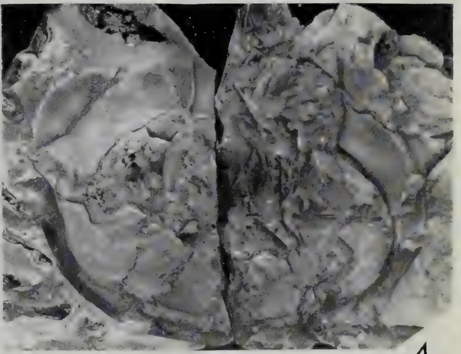
Member D, Ngorora Formation, Miocene ; Kalimale, Kenya

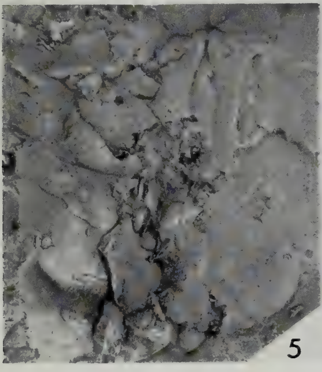
FIG. 2. Kenya National Museum. Merus and carpus of left cheliped showing single carpal spine. × 1·75.

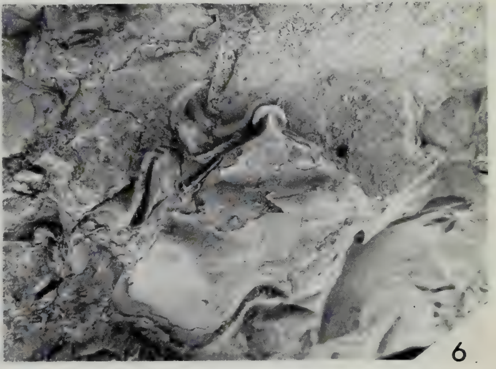

1


2


3


4


5


6

CYCLOTHYRIS (CRETACEOUS BRACHIOPODA) FROM CALIFORNIA

By ELLIS F. OWEN

ABSTRACT

Serial sections confirm the occurrence of *Cyclothyris densleonis* in the Upper Cretaceous of North America; the known distribution of the genus is extended to California.

Mesozoic brachiopods have not been extensively described within the North American continent, and it is not surprising that little interest has been shown by palaeontologists in the few species of Rhynchonellidae and Terebratulidae already established in the literature. If, on the other hand, some of these records are further investigated, they can provide useful information regarding the ubiquitous nature of some genera and species of little-known distribution.

Among early records of brachiopods from beds of known Cretaceous age are those of Whiteaves (1876–1903) and Anderson (1902, 1958) who described rhynchonelloid brachiopod species which they referred broadly to the genus *Rhynchonella*. More recently Imlay (1937) described a species from the Lower Cretaceous of Mexico which he referred to *Cyclothyris* ? *subtrigonalis*. This was the first citation, albeit tentative, of the genus *Cyclothyris* from the American continent, but the accompanying transverse serial sections of the species do not support its assignment to this genus.

It was not until 1955 that Cooper, in a description of some brachiopods from the Cretaceous of Arizona, first accurately recorded the genus *Cyclothyris* from North America, describing and figuring a species as *C. americana* from the Mural Limestone (Middle Albian) of the Bisbee Quadrangle. Until this positive record, the genus was considered to have been confined to the Cretaceous of western Europe and England where it is represented by species from the Aptian to Upper Cenomanian.

Anderson (1902) described and figured a rhynchonellid as *Rhynchonella densleonis* from the Middle Cretaceous of Shasta County (Horsetown Group), northern California. Later, in a description of Cretaceous beds of the Pacific coast (Anderson 1958), he considered that beds within the Horsetown Group yielding *R. densleonis* were no younger than Lower Cenomanian in age and that their probable range was from Upper Albian to Lower Cenomanian. A specimen of *R. densleonis* Anderson has recently been obtained from the type section and is described here. From the internal structures seen in transverse serial sections of a specimen (Fig. 4), it can be positively assigned to *Cyclothyris*.

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 301–304 *Issued* 28 *October* 1976

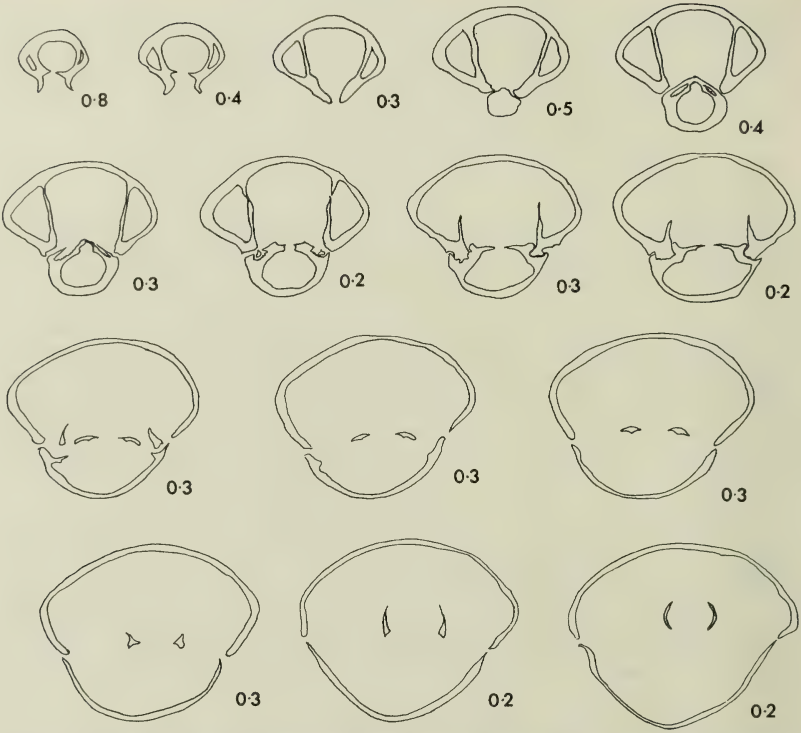


FIG. 4. A series of fifteen transverse serial sections through the umbo of a duplicate specimen of *Cyclothyris densleonis* Anderson from the Horsetown Group (Albian–Cenomanian), Shasta County, California. Geological Survey of America Locality No. 1051. The encircling deltidial plates around the foramen, the comparatively short dental lamellae and general morphology of the hinge-plates are typical of the genus. The numerals denote the distance in millimetres between each section. × 3.

SYSTEMATIC DESCRIPTION

Family **RHYNCHONELLIDAE** Gray 1848

Subfamily **CYCLOTHYRIDINAE** Makridin 1955

Genus ***CYCLOTHYRIS*** M'Coy 1844

Cyclothyris densleonis (Anderson)

Fig. 4; Pl. 5, figs 1–6

1902 *Rhynchonella densleonis* Anderson : 72 ; pl. 7, figs 157, 158.
1958 *Rhynchonella densleonis* Anderson ; Anderson : 86 ; pl. 1, figs 3, 4.

DESCRIPTION. *External characters.* Acutely biconvex *Cyclothyris*, 17·2 mm long, 20 mm wide, 11·9 mm thick. Broadly triangular in general outline. The brachial valve is slightly inflated ; the pedicle valve has a broad, shallow sulcus originating from about the mid-line and widening anteriorly with a fairly extensive trapezoidal linguiform extension. Shell ornament consists of numerous radiating fine costae or costellae which are affected by a series of marked marginal plications creating a distinctive ornament ; similar ornament is characteristic of *Cyclothyris antidichotoma* (Buvignier) from the Upper Aptian and Lower Albian of France and England. The umbo is slightly produced and the sharp beak suberect. Distinct beak-ridges border an extensive interarea with exposed deltidial plates encircling a medium-sized foramen.

Internal characters. The series of transverse serial sections given here (Fig. 4) for *C. densleonis* have been compared to those of *Cyclothyris latissima* (J. de C. Sowerby), the type-species from Faringdon, Berkshire, as figured by Owen (1962 : 46). The two series of sections appear almost identical in every detail. The characteristic deltidial plates encircling the foramen are shown to perfection, as well as the comparatively short dental lamellae in the pedicle valve. The shape, length and angle of deflection of the hinge-plates also agree, as do the depth of insertion and general quadrate shape of the hinge-teeth.

REMARKS. There is an unmistakable similarity between *C. densleonis* (Anderson) and *C. antidichotoma* (Buvignier), but it differs from the latter species in having finer and more numerous costellae, a more acutely triangular general outline, a narrower fold and sulcus, a more inflated brachial valve and considerably smaller overall dimensions. The marginal plicae in *C. densleonis* appear to be more marked within the sulcus and on the faint or incipient brachial fold, where there are usually three or four.

In general outline it is more readily comparable to *Cyclothyris mirabilis* (Walker) from the Lower Albian of Leighton Buzzard, Bedfordshire, but differs in having more, but less acutely developed, marginal plicae, and a slightly more produced umbo ; it is less inflated than *C. mirabilis*.

A species which shows a closer morphological affinity with the American form was described and figured by Panow (1969) as ? *Cyclothyris antidichotoma* (Buvignier), and occurs in Lower Cenomanian beds in the Cracow district of Poland. The specimen figured by Panow (1969 : pl. 109, fig. 9) has a wider anterior sulcus, a slightly less extensive linguiform extension, a less produced umbo and a less acutely inflated brachial valve.

The importance of the present record is that it confirms that of Cooper (1955) in establishing *Cyclothyris* within the Albian and Cenomanian of North America and extends the distribution of that genus to include California. It may be possible in time to investigate the records of other workers, such as Whiteaves (1876–1903), so that a clearer view of the distribution of *Cyclothyris* and similar brachiopod genera may be obtained.

REFERENCES

ANDERSON, F. M. 1902. Cretaceous deposits of the Pacific coast. *Proc. Calif. Acad. Sci.*, San Francisco, (3) **2** 1 : 1–129, 12 pls.

ANDERSON, F. M. 1958. Upper Cretaceous of the Pacific coast. *Mem. geol. Soc. Am.*, New York, **71** : 1–378, 75 pls.

COOPER, G. A. 1955. New Cretaceous Brachiopoda from Arizona. *Smithson. misc. Collns*, Washington, **131** 4 : 1–18, 4 pls.

IMLAY, R. 1937. Lower Neocomian fossils from the Miquihuana region, Mexico. *J. Paleont.*, Chicago, **11** 7 : 552–574, 14 pls.

OWEN, E. F. 1962. The brachiopod genus *Cyclothyris*. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **7** 2 : 39–63, 2 pls.

PANOW, E. 1969. Contribution to the knowledge of the brachiopods from the Upper Cretaceous of the Krakow district. *Roczn. pol. Tow. geol.*, Krakow, **39** 4 : 555–608, 4 pls.

WHITEAVES, J. E. 1876–1903. *Mesozoic Fossils* **1** : 1–415, 51 pls. Ottawa (Geol. Surv. Canada).

E. F. OWEN, M.Phil., M.I.Biol., F.L.S.
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

Accepted for publication 9 February 1976

PLATE 5

Prefix BM(NH) – British Museum (Natural History), London
MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland

Cyclothyris densleonis (Anderson)

FIG. 1a, b, c. Cretaceous, Horsetown Group, Shasta County, northern California. BM(NH) BB 76200. × 2.

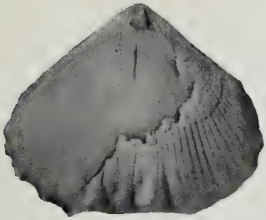
FIG. 4a, b, c. Same locality and horizon. BM(NH) BB 76201. × 2.

Cyclothyris antidichotoma (Buvignier)

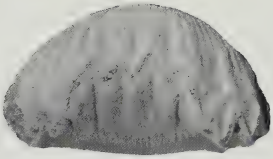
FIG. 2a, b, c. Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. BM(NH) BB 41495. × 1.

FIG. 2d. Enlargement of margin of shell of the same specimen as above, showing the typical *antidichotoma* ornament. × 2.

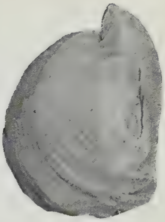
FIG. 3a, b. Albian, Morteau, Doubs, France. Internal mould of a young specimen. MHNG CB 4746. × 2.



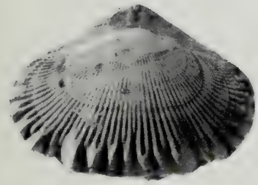
1a



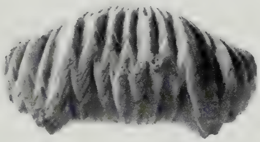
1c



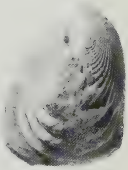
1b



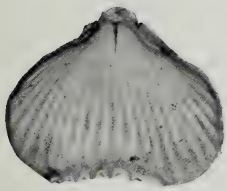
2a



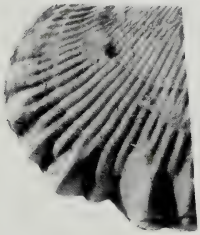
2c



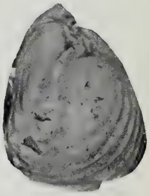
2b



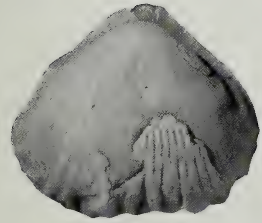
3a



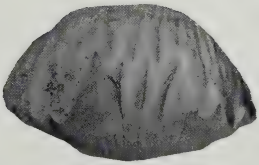
2d



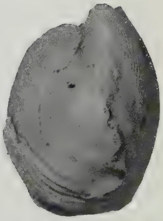
3b



4a



4c



4b

CRANIAL MATERIAL OF OLIGOCENE AND MIOCENE FLAMINGOS: WITH A DESCRIPTION OF A NEW SPECIES FROM AFRICA

By C. J. O. HARRISON & C. A. WALKER

ABSTRACT

Cranial material is available for two mid-Tertiary flamingos, *Phoenicopterus croiseti* from the Oligocene and a new species from the Miocene, and this is compared with skulls of the three Recent genera. The skull of *P. croiseti* from the Upper Oligocene of France is partly reconstructed, using additional material. It is sufficiently distinct from the type species of *Phoenicopterus*, the Recent *P. ruber*, to warrant its designation as the type species of a new genus, *Gervaisia*. Its bill is slender and less decurved than in *Phoenicopterus*, the mandibular symphysis is shorter and the upper jaw is broad to the tip. New flamingo material from the Lower Miocene of Rusinga Island, Kenya, is referred to *Phoenicopterus* on the basis of palate structure. It is specifically distinct from *P. ruber*, the bill-shape being different and the size much smaller, and it is therefore described as a new species, *P. aethiopicus*.

INTRODUCTION

THE RECENT flamingos comprise four species separated into three genera, *Phoenicopterus*, *Phoeniconaias* and *Phoenicoparrus*, the last including both *P. jamesi* and *P. andinus*. *Phoenicopterus ruber* has three separate populations, *P. r. antiquorum* in Eurasia and Africa, *P. r. ruber* in the Caribbean and Central America and *P. r. chilensis* in southern South America. These are sometimes treated as separate species, but their bones differ only in size. All three forms have been used here for comparison but the skull of the last, *Phoenicopterus ruber chilensis*, has been chosen for the figures.

Skulls representing the three genera were available for examination and are shown in lateral view (Fig. 5B–D). These are *Phoenicopterus ruber*, *Phoeniconaias minor* and *Phoenicoparrus jamesi* respectively. The three, in that order, show a progressive modification of the bill, probably linked with different feeding methods. In the first two we know of such differences, *Phoenicopterus ruber* being a more generalized feeder, on minute crustacea for the most part, and *Phoeniconaias minor* a more specialized feeder on blue-green algae. The bill-structure of *Phoenicoparrus* suggests a feeding method involving fine filtering similar to that of *Phoeniconaias*.

The most generalized form, *Phoenicopterus*, has a longer and less angled bill. In the other two the lower mandible is stouter and shorter and is deflected downwards more vertically; the bony structure is more laterally inflated and the mandibular symphysis longer. At the same time the upper jaw is laterally narrow (Fig. 6), and more sharply angled (Fig. 5), while the palatal ridge is a narrower and deeper wedge (Fig. 7). It is apparent that for the three Recent genera the palate and bill structure are diagnostic features, and cranial material of fossil species can be compared with

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 305–314 *Issued* 28 *October* 1976

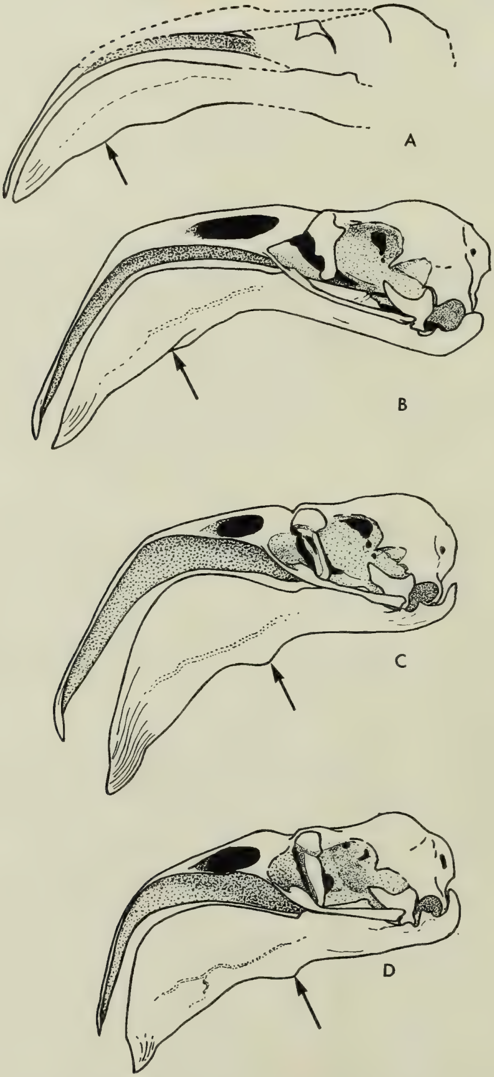


FIG. 5. Lateral views of skulls of: A, *Gervaisia croiseti* (after Gervais); B, *Phoenicopterus ruber chilensis*; C, *Phoeniconaias minor*; D, *Phoenicoparrus jamesi*. The small arrows indicate the posterior margin of the mandibular symphysis; the shaded portions of the upper mandible indicate the area of the palate visible laterally.

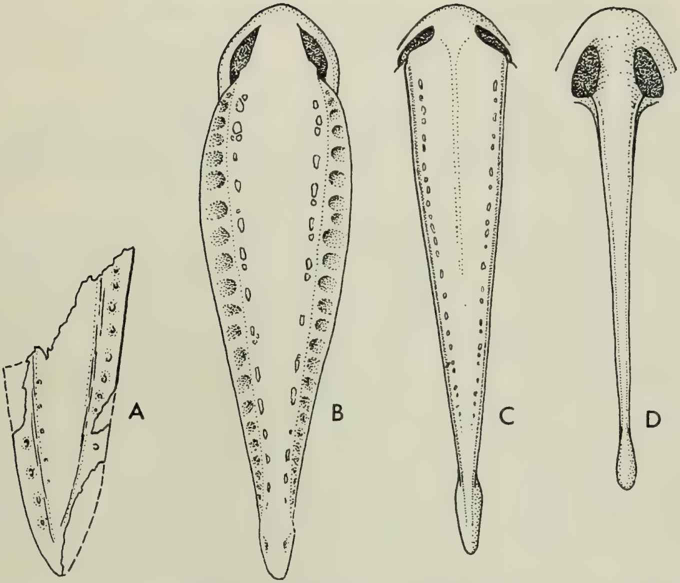


Fig. 6. Anterior views of upper mandibles of: A, *Gervaisia croiseti* (after Gervais); B, *Phoenicopterus ruber chilensis*; C, *Phoeniconaias minor*; D, *Phoenicoparrus jamesi*.

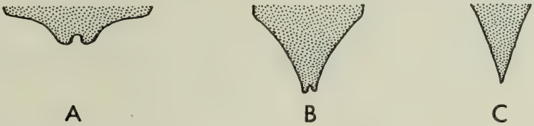


Fig. 7. Transverse section of palate, level with anterior end of nares, of: A, *Phoenicopterus ruber*; B, *Phoeniconaias minor*; C, *Phoenicoparrus jamesi*.

these. Cranial material of fossil flamingos is available for only two forms, *Phoenicopterus croiseti* and a new form from Africa.

GERVAISIA

Phoenicopterus croiseti Gervais 1852

Figs 5A, 6A

P. croiseti was described by Gervais from parts of two skulls and a tarsometatarsus from Clermont-Ferrand and Gergovie, Puy-de-Dôme, France. The deposits at these localities are now thought by Thenius (1959) to be Upper Oligocene and not Lower Miocene as originally stated. More recently a specimen in the collection of the British Museum (Natural History) has been prepared; it is no. A 2665 (*ex*

27827), from the Croiset Collection purchased in 1848, and though said to be collected at Pérignat, France, it is inscribed 'Gergovie'. The preparation has exposed most of the anterior part of a lower mandible and a separate small portion of the posterior end of the mandible in the region of the coronoid process. The mandibular symphysis has undergone some lateral crushing. In shape, size and age the specimen is referable to the present species. With the help of it, using Gervais's plates but not his original specimens, it has been possible to reconstruct part of the skull of *P. croiseti* (Fig. 5A).

The cranial region is too incomplete to be useful, but the bill shows distinctive characters (Figs 5A, 6A). It is longer, narrower and less abruptly decurved than the bills of Recent species. The BM(NH) specimen appears deeper towards the tip of the lower mandible, but the broad tip of the upper jaw, present in Gervais's specimen, may cause the rami of the lower mandible to diverge more sharply dorsally and appear shallower in lateral view. As shown by the BM(NH) specimen the lower mandible is not only narrower and straighter than those of Recent species, with a shorter symphysis as indicated by the small arrows in Fig. 5, but the bony structure is also less inflated. That of *Phoenicopterus* shows distinct lateral inflation of the bone, especially in the deep mid-section of the mandible, and this inflation increases in *Phoenicoparrus* and *Phoeniconaias*. The posterior fragment of lower mandible (A 2665), which includes the coronoid process, has been crushed and provides little information other than that the process appears to have been well developed and that the foramen a little below the process was present.

The palatal ridge of *P. croiseti* is shallow and the upper jaw is down-curved but not angled. The end of the upper jaw differs from those of other flamingos in being broad right to the tip, those of the series of three Recent species listed above showing increased lateral constriction (Fig. 6).

From the shape of the bill *P. croiseti* would appear to have had a more generalized method of feeding than living flamingos. It differs more from the three extant genera than they differ between themselves. If the others are separated into different genera then *croiseti* requires a genus of its own. Apart from the cranial material we have little information on it; the limb bones referred to this species by Gervais (1852), Milne-Edwards (1867–71) and Lydekker (1891) are similar in size and structure to those of *Phoenicopterus ruber* and are not outstandingly diagnostic. The following new genus is proposed.

GERVAISIA gen. nov.

Etymology. The genus is named after Paul Gervais who first described the species. It is feminine in gender.

Type species. *Phoenicopterus croiseti* Gervais 1852 : 233–234 ; pl. 2, figs 4–5.

Diagnosis. Bill long and slightly decurved but not angled. Palatal ridge shallow and apparently absent from anterior third of upper jaw. Upper jaw broad and dorsoventrally flattened towards the tip, tapering only gradually. Similar in size to *Phoenicopterus ruber*.

Occurrence. Transitional Oligocene/Miocene deposits of France and Germany (Brodkorb 1963 : 272).

A NEW LOWER MIOCENE AFRICAN FLAMINGO

The collection of the British Museum (Natural History) contains some fragmentary avian material from the Lower Miocene of Rusinga Island in the Kenyan waters of Lake Victoria. A number of these fragments, mostly ends of long bones, appear referable to a single species of small flamingo, similar in size to the Recent *Phoeniconaias minor*. They consist of two mandibular fragments, one proximal and three distal ends of humeri, one distal end of a femur, three distal ends of tibiotarsi, and five proximal and two distal ends of tarsometatarsi. The limb bones, which are mostly broken or crushed to some degree, show little difference from those of *Phoeniconaias minor* save that an almost complete proximal end of a tarsometatarsus shows the calcaneal ridges of the hypotarsus to be similar in proximal view to those of Recent species but only half to two-thirds their length.

The jaw fragments, however, differ more from *Phoeniconaias minor* in their structure. The larger fragment (Figs 8A, 9A) is the posterior part of the upper jaw with most of the narial apertures, embedded in matrix at its posterior end. Its most significant feature is the poorly-developed palatal projection with the double ridge along its centre. In this respect it resembles *Phoenicopterus ruber* so closely that it seems reasonable to include it in that genus (Fig. 9A–B).

The other fragment is from the anterior end of the lower jaw. It is slender, slightly decurved, and heavily grooved in a manner more similar to that of *Phoeniconaias*. It tapers more gradually than does the bill of *Phoenicopterus ruber* in this region and may therefore have been longer and more slender ; it appears less deeply hollowed ventrally towards the posterior and in comparison with *P. ruber* the bill may have been shallower in the region of the symphysis. The most marked

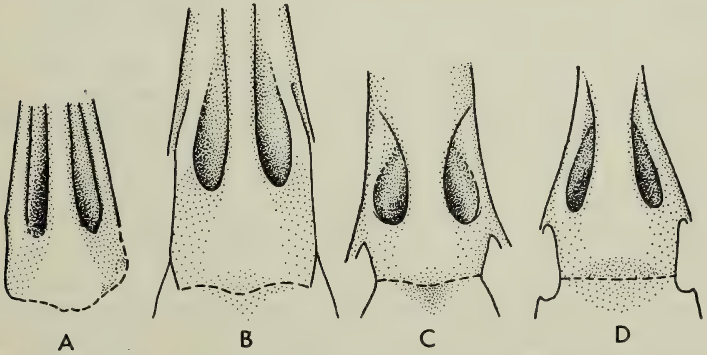


Fig. 8. Dorsal views of basal area of upper mandibles of : A, *Phoenicopterus aethiopicus* (holotype) ; B, *Phoenicopterus ruber chilensis* ; C, *Phoeniconaias minor* ; D, *Phoenicoparrus jamesi*.

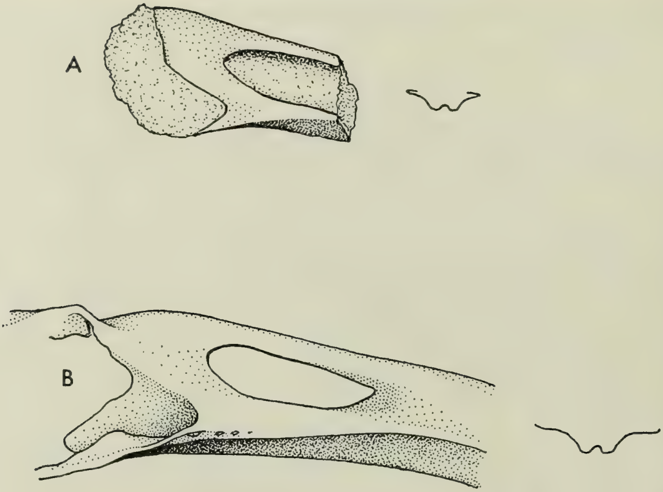


Fig. 9. Lateral (right) view of posterior part of upper jaw and transverse section of palatal ridges of: A, *Phoenicopterus aethiopicus*; B, *P. ruber chilensis*.

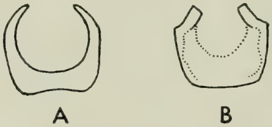


Fig. 10. Transverse section of lower mandible, near tip, of: A, *Phoenicopterus ruber chilensis*; B, *Phoenicopterus aethiopicus* (holotype) partly concealed by matrix.

difference however is in the shape of the tomial edge of this region of the mandible. Recent species of flamingo, and as far as can be determined this applies also to *Gervaisia croiseti*, have a flattened dorsal edge to the tomium on which the flat edge of the upper jaw rests, although the latter is much reduced in *Phoenicoparrus* and *Phoeniconaias*. *Phoenicopterus ruber* has slender, incurving tomia on the lower jaw (Fig. 10A). The new species has stout tomia slanting inwards on the inner surface, with a sharp dorsal ridge, and the outer surface bordering this ridge is laterally compressed to produce a shallow hollow (Fig. 10B). The general appearance suggests that the anterior end of the upper jaw, at present unknown, may have overlapped the lower jaw. If this were so it would constitute a unique feature within the Phoenicopteridae and further taxonomic separation of this species might be justified. For the present, in view of the palatal similarity and the lack of confirmation of possible differences, we propose to treat this as a new species of the genus *Phoenicopterus*.

Phoenicopterus aethiopicus sp. nov.

Figs 8A, 9A, 10B ; Pl. 6

ETYMOLOGY. The species is named after the continent in which it occurs.

DIAGNOSIS. Small, slightly smaller than *Phoeniconaias minor*. Palatal ridge shallow and double, very similar to that of *Phoenicopterus ruber*. Tip of lower jaw narrow, slender and heavily grooved and with stout tomia compressed along the external side to produce a shallow groove, the appearance of which suggests that it might accommodate tomia of upper jaw. Tarsometatarsus with calcaneal ridge of hypotarsus short.

MATERIAL. Holotype : the posterior part of an upper jaw, BM(NH) Pal. Dept. No. A 4382. Paratypes : BM(NH) Nos A 4383–4398, comprising the distal part of a lower jaw, two distal and five proximal ends of tarsometatarsi, three distal ends of tibiotarsi, one distal end of a femur, and three distal and one proximal end of humeri. Most material partly damaged or crushed. Collected and presented by the late Dr L. S. B. Leakey in 1935.

OCCURRENCE. Lower Miocene ; locality Rs 12, Rusinga Island, NE Lake Victoria, Kenya.

DESCRIPTION. The holotype is the posterior portion of an upper jaw broken short proximal to the anterior end of the nares, and with some shattering of the internasal bridge. The posterior end terminates at the frontonasal hinge, where it is embedded in matrix. The bone is slender, widening dorsally at the posterior end. The culmen shows only slight curvature and is a little flattened where it terminates posteriorly. The nares are elongated and of fairly even width, rising slightly at the posterior end. The palate is flat posteriorly, with shallow paired ridges present along most of the length and increasing in depth anteriorly.

The anterior end of the lower jaw (A 4384) is within the region of the symphysis and lacks the tip. It is slender, rounded and slightly decurved. Proximally it is flattened and slightly hollowed ventrally. Both ventral surface and sides have many deep longitudinal grooves. The internal surfaces are concealed by matrix, but the interior is deeply hollowed, with incurving tomia. The latter are thicker than those of *P. ruber* and project dorsally, the edges forming dorsal ridges. The sides of the jaw bordering the tomia are laterally compressed to form on each side a shallow hollow with a prominent lower margin, its appearance suggesting that the tomia of the upper jaw may have overlapped it.

On the tarsometatarsus the hypotarsus is very short proximodistally, differing in this respect from those of Recent species and from the similar-sized *P. minutus* Howard 1955 of the Upper Pleistocene of California. The distal end of the tarsometatarsus is like that of *Phoeniconaias*, differing from that of *P. novaehollandiae* A. H. Miller 1963 of the Australian Miocene in the greater spread of trochleae and less clearly indicated articulation for digit 1, from *P. floridanus* Brodkorb 1953 of the Florida Lower Pliocene in the proximally shorter trochlea for digit 2, and *Phoeniconaias gracilis* A. H. Miller 1963 of the Australian Early Pleistocene in the rounder and broader trochlea for digit 2 and more extensive articular surface on the trochlea for digit 4. The present species also differs from *P. floridanus* in having the distal end of the tibiotarsus narrower posteriorly, and from *P. stocki* L. Miller 1944 of the Mexican Middle Pliocene in being proportionally narrower across the anterior intercondylar groove of this bone. The other known fossil flamingos, *Phoeniconotius eyrensis* A. H. Miller 1963 of the Australian Miocene and *Phoenicopterus copei* Shufeldt 1891 (see Shufeldt 1892) of the American Middle Pleistocene, are both considerably larger species. Except in the matter of size, however, the known differences between these various species are slight, and where critical cranial material is absent it is impossible to assess the true affinities adequately.

MEASUREMENTS. Holotype, A 4382 : dorsal length 27·2 mm ; ventral length 28·1 mm ; depth at posterior end 17·0 mm, at posterior end of nares to tomium 11·5 mm, to palate 14·3 mm, depth at anterior end to tomium 8·5 mm, to palate 11·4 mm ; width of nares 5·7 mm ; width of posterior nasal strut 5·3 mm.

Anterior portion of lower jaw, A 4384 : length 26·1 mm ; posterior width 12·4 mm, depth 9·8 mm ; width between tomia posteriorly 5·0 mm ; anterior width 7·8 mm, depth 7·5 mm ; width between tomia anteriorly 4·2 mm ; depth of lateral compression bordering tomia 2·2 mm.

Proximal end of tarsometatarsus, A 4383 : width at proximal end 14·0 mm ; width of hypotarsus 7·9 mm ; anteroposterior depth of proximal end to hypotarsus 15·8 mm ; depth of cotyla 8·6 mm ; proximodistal length of external calcaneal ridge 8·8 mm, of internal ridge 8·6 mm.

ACKNOWLEDGEMENTS

We wish to thank Miss M. L. Holloway of the British Museum (Natural History) for preparing the line drawings.

REFERENCES

BRODKORB, P. 1953. A Pliocene flamingo from Florida. *Chicago Acad. Sci. nat. Hist. Misc.* **124** : 1–4, 2 figs.

—— 1963. Catalogue of fossil birds, part 1. *Bull. Fla St. Mus. biol. Sci.*, Gainesville, **7** 4 : 179–293.

GERVAIS, P. 1848–52. *Zoologie et Paléontologie Françaises*, **1.** 271 pp. Paris.

HOWARD, H. 1955. Fossil birds from Manix Lake, California. *Prof. Pap. U.S. geol. Surv.*, Washington, **264-J** : 199–206, pl. 50.

LYDEKKER, R. 1891. *Catalogue of the fossil birds in the British Museum* (*Nat. Hist.*). xxvii + 368 pp., 75 figs. London.

MILLER, A. H. 1963. The fossil flamingos of Australia. *Condor*, Santa Clara, Calif., **65** : 289–299, 6 figs.

MILLER, L. 1944. A Pliocene flamingo from Mexico. *Wilson Bull.*, Sioux City, Iowa, **56** : 77–82, 2 figs.

MILNE-EDWARDS, A. 1867–71. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France.* 474 + 632 pp., atlas 200 pls (2 vols). Paris.

SHUFELDT, R. W. 1892. A study of the fossil avifauna of the Equus Beds of the Oregon desert. *J. Acad. nat. Sci. Philad.* (2) **9** : 389–425, pls 15–17.

THENIUS, E. 1959. *Handbuch der stratigraphischen Geologie*, **3**, Tertiär. Teil 2, Wirbeltierfaunen. xi + 328 pp. Stuttgart.

Dr C. J. O. Harrison, Ph.D.
Subdepartment of Ornithology
British Museum (Natural History)
Tring
Herts

C. A. Walker
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

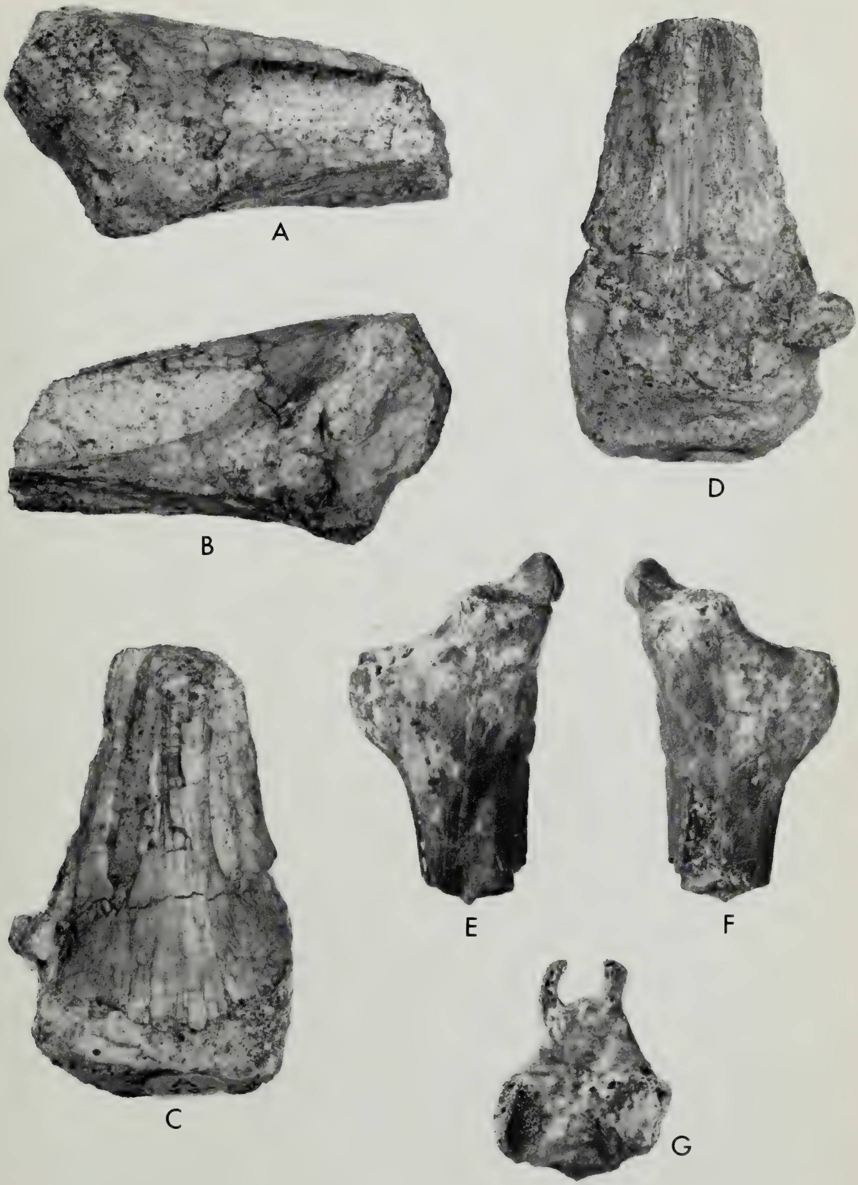
Accepted for publication 9 February 1976

PLATE 6

Phoenicopterus aethiopicus sp. nov.

Holotype, BM(NH) A 4382. Views of the posterior portion of the upper jaw, × 2. A, right lateral. B, left lateral. C, dorsal. D, palatal.

Paratype, BM(NH) A 4383. Views of the proximal end of a right tarsometatarsus, × 2. E, external. F, internal. G, proximal.


A
B
D
E
F
C
G

A NEW FOSSIL PELICAN FROM OLDUVAI

By C. J. O. HARRISON & C. A. WALKER

ABSTRACT

A new species of fossil pelican, *Pelecanus aethiopicus*, based on a tarsometatarsus and a scapula (both incomplete), is described from the Middle Pleistocene of Olduvai, Tanzania. It is compared with Recent and fossil forms.

In the collection of the Department of Palaeontology of the British Museum (Natural History) are several fragments of bird bones collected from the Middle Pleistocene deposits at Olduvai, Tanzania. All the specimens are of birds associated with an aquatic environment, and are referable to Recent genera, but some may be sufficiently different from present-day forms to make it necessary to consider them as separate species. One such is the proximal part of a tarsometatarsus of a pelican which might have been a forerunner of one or more Recent species within the genus concerned.

Order PELECANIFORMES Sharpe
Suborder PELECANI Sharpe
Family **PELECANIDAE** Vigors
Genus ***PELECANUS*** Linnaeus
Pelecanus aethiopicus sp. nov.
Plate 7

Diagnosis. Proximal end of tarsometatarsus having internal edge of anterior surface with posterior curvature and with smooth, not abrupt slope to lip of internal cotyla. On internal anterior edge, the ridge marking proximal edge of ligamental furrow curves posteriorly only a little distal to level of hypotarsus. Distal edge of posterior aperture of inner proximal foramen only just proximal to level of distal edge of hypotarsus. Hypotarsus posteriorly prominent on internal side, with sharp slope towards internal side. Internal calcaneal ridge stout, with head only slightly prominent distally, and with slight ridge towards internal edge. Triangular bridge, tapering distally, over second tendinal groove formed by heads of next two calcaneal ridges. Internally the edge of this triangular head begins only a little anterior to edge of head of internal calcaneal ridge, and slopes externally, with some anterior curvature. External tendinal groove accommodated laterally, on the external side of hypotarsus, rather than on posterior surface (Fig. 11).

Material. Holotype, proximal end of a right tarsometatarsus, British Museum (Natural History) Palaeontology Dept. No. A 4291. Paratype, proximal end of a right scapula, No. A 4292 in the same collection.

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 315–320 *Issued* 28 *October* 1976

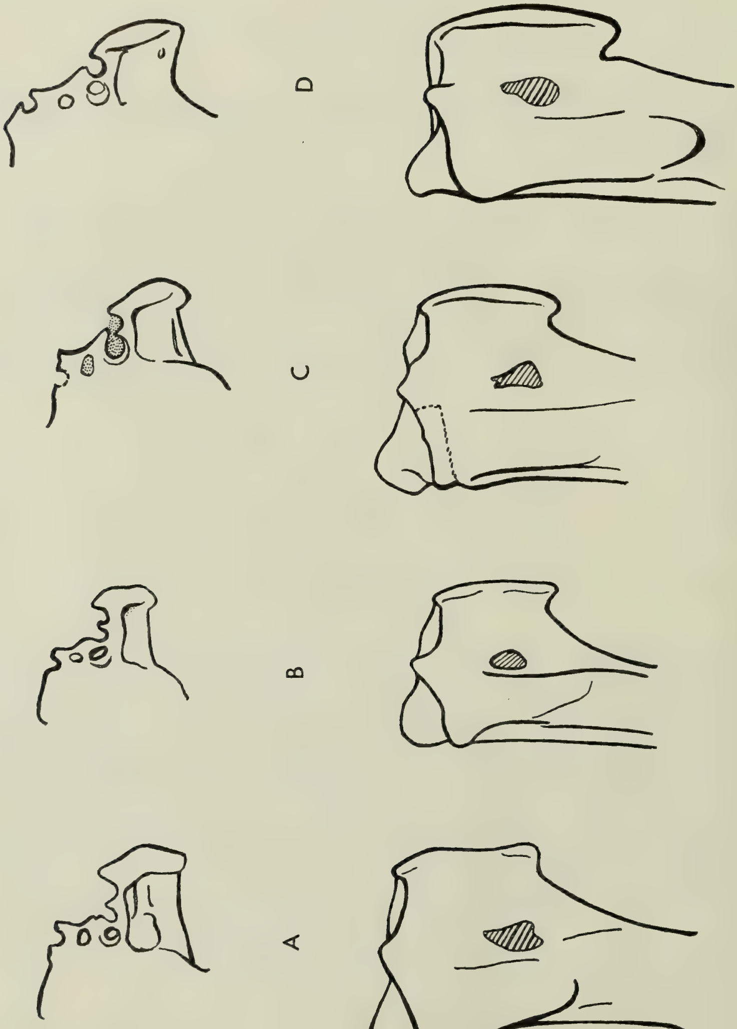


FIG. 11. Anterior and internal views of proximal end of right tarsometatarsi. A, *P. crispus*; B, *P. rufescens*; C, *P. aethiopicus* sp. nov., BM(NH) No. A 4291; D, *P. onocrotalus*.

Locality and Horizon. Bed I, site FLKS, Olduvai Series (Middle Pleistocene), Olduvai Gorge, Tanzania (Leakey 1965 : 102). Collected and presented by the late Dr L. S. B. Leakey, 1935.

Description. The holotype is the proximal end of a right tarsometatarsus (Fig. 11C) in good condition, but with the tendinal canals and anterior fossa filled with matrix and some crushing of the shaft distally. The external surface is broad and flat, terminating posteriorly in a distinct ridge, and anteriorly forming a more rounded ridge bordering the anterior fossa. The anterior surface has a distinct median metatarsal groove deepening towards the occluded fossa. At the distal edge of the fossa there is a small tibialis anticus tubercle on the inner side and a smaller ancillary pit next to it on the external side.

The internal edge is more smoothly rounded than the external edge and shows some posterior curvature distally. At the proximal end it widens to accommodate a broad, short hollow just below the lip of the cotyla, presumably for the attachment of the proximal ligament ; the inner edge of this projects inwards across the proximal edge of the fossa. The more distal part of the internal edge is smoothed away where a ligamental band would have crossed it, this surface terminating proximally in a small ridge a little below the level of the tibialis anticus scar and curving posteriorly across the internal side (Fig. 11C).

The internal surface is slightly curved and narrow proximally, to widen again just below the lip of the internal cotyla, which is broken in the present specimen. The proximal surface is roughly rectangular. The intercotylar prominence is elevated and bluntly rounded. Viewed anteriorly, it shows some external deflection ; viewed laterally it shows slight anterior prominence, continuing the line of the inner edge of the proximal ligamental attachment hollow, and dorsally slopes gradually towards the hypotarsus. The internal cotyla is narrower laterally and concave with a slight anterior tilt. The external cotyla is narrow and slopes anteriorly, its anterior edge curving down towards the anterior fossa. There is a narrow slanting intercotyla depression at the posterior inner edge of the internal cotyla, and a narrow, shallow groove crosses the posterior edge of this cotyla and extends to the opening of the second tendinal canal.

The hypotarsus is large and stout. The main structure is the internal calcaneal ridge which is thick and prominent, although extending less far proximodistally than those of some *Pelecanus* species. Its posterior surface is flattened, projecting a little at the edges and sloping externally with a slight longitudinal ridge towards the internal side. Distally, below this overhanging surface the calcaneal ridge extends distally, decreasing in height. The internal surface of the ridge is irregular with small ridges and foramina. The posterior aperture of the inner proximal foramen, at the base of the inner calcaneal ridge just below the projecting surface, is large and irregular in shape. The anterior surface of the inner calcaneal ridge is concave, with a narrow projecting external edge.

On the external side of the large inner calcaneal ridge there are two tendinal canals, one above the other, only one showing between the edge of the posterior surface of the ridge and the edge of the surface roofing the next tendinal canal. The second lateral tendinal canal, between the middle and outer calcaneal ridges, is roofed over. The middle calcaneal ridge is much shorter and slimmer than the inner, and only half as long. The roof of these forms a triangular-shaped surface, tapering distointernally and with a hollow above the tendinal canal, and has an external slant. The posterior opening of the outer proximal foramen is just distal and external to the posterior opening of the second tendinal groove. On the external side of the external calcaneal ridge there is a shallow lateral groove, a second groove diverging anteriorly from the distal end of this and passing across the proximal posterior corner of the external surface. Both these latter grooves are small and poorly defined, with a slight ridge between them which is eroded in the specimen.

The paratype is the proximal end of a right scapula with furcular articulation broken off short, at a level with the eroded coracoid articulation. The shaft shows some crushing. The coracoid articulation is a prominent rounded facet projecting beyond the line of the anterior edge. The glenoid facet, which slants proximo-internally, is oval and elongate, with a small prominent lip along its outer edge, and a concavity in the bone on the dorsal surface above it.

MEASUREMENTS (in millimetres). (a). Holotype: proximal end of a right tarsometatarsus, BM(NH) No. A 4291.

Maximum length as preserved	53·9
Maximum width across cotyla	24·5
Minimum measurable width	16·2
Depth of hypotarsus	29·5
Depth at internal cotyla	15·5
External depth of distal end to central posterior ridge	19·3
Internal depth of distal end to central posterior ridge	15·6
Depth of external side at level of tibialis anticus scar	13·4
Depth of internal side at level of tibialis anticus scar	9·9
Length of cap of internal calcaneal ridge	20·7
Maximum width of cap of internal calcaneal ridge	11·2
Length of second calcaneal ridge	16·0

(b) Paratype: proximal end of a right scapula, BM(NH) No. A 4292.

Maximum length of scapula as preserved	45·1
Maximum width	26·2
Width to internal edge of coracoid articulation	24·0
Width of coracoid articulation	10·2
Maximum thickness of shaft	5·9
Width of shaft	11·3
Width of glenoid facet	8·6
Length of glenoid facet	14·0

COMPARISON AND COMMENTS. The following Recent specimens were available for examination. *Pelecanus crispus* 5, *P. rufescens* 1, *P. conspicillatus* 2, *P. onocrotalus* 8, *P. erythrorhynchus* 1, *P. occidentalis* 5. Of these, *crispus* (Fig. 11A), *rufescens* (Fig. 11B) and *conspicillatus* differ from *aethiopicus* in having on the external side of the large internal calcaneal ridge a series of three tendinal grooves of which the outer two are open, and in having a more posteriorly prominent calcaneal ridge. *P. erythrorhynchus* differs from *aethiopicus* in having the three tendinal grooves and a proximodistally long calcaneal ridge like that of *onocrotalus* but less abrupt distally. Its internal calcaneal ridge is, however, stout and only projects a short distance.

P. onocrotalus differs from *aethiopicus* in its stouter, less projecting, and proximodistally longer internal calcaneal ridge, and in its broader and less projecting hypotarsus. *P. occidentalis* is peculiar in that two discrete populations have different hypotarsi. The North and Central American population differs from *aethiopicus* in having the hypotarsus narrow and prominent, with two open tendinal canals posterior to a closed one, the more anterior of the two being partly enclosed. The southern population, *P. o. thagus* of Chile and Peru, is a larger form in which the hypotarsus is much stouter and projects less. The external edge of the internal calcaneal ridge is extended externally, projecting beyond the tendinal canals. The two open posterior canals become displaced anteriorly and the more anterior of the two is completely enclosed. The general effect is as though the hypotarsus had been compressed onto the tarsometatarsal shaft with accompanying distortion. In view of this divergence in what is otherwise a specifically constant character there may be grounds for re-examining all characters of the two forms of *occidentalis* to determine whether their earlier separation as two species may be preferable. Both forms differ from *aethiopicus* in the characters mentioned.

Hypotarsal material is available for only a few fossil pelicans. *P. gracilis* Milne-Edwards 1867, *P. intermedius* Fraas 1870 and *P. odessanus* Widhalm 1886 (listed by Lambrecht 1933 : 279) all have the narrower and more projecting hypotarsus typical of the *crispus* group ; on the last two the two open posterior tendinal grooves are apparent. The first two of these species are from the Miocene, the last from the Lower Pliocene. Of the three Pleistocene species already known *P. halieus* Wetmore 1933 from North America, described from a radius, is very small and osteologically similar to *erythrorhynchus*, the Recent North American species. *P. grandiceps* De Vis 1906 and *P. proavus* De Vis 1892 (p. 444), found in Australia and described as similar to *conspicillatus*, the only Recent species occurring in that region, were described from various bones among which the proximal ends of tarsometatarsi were not represented. Present information suggests *aethiopicus* differs from all of these.

ACKNOWLEDGEMENTS. We would like to thank Miss M. L. Holloway for making the line drawings, and Mr C. Keates for taking the photographs.

REFERENCES

DE VIS, C. W. 1892. Residue of the extinct birds of Queensland as yet detected. *Proc. Linn. Soc. N.S.W.*, Sydney, (2) **6** : 437–456 ; pls 23–24.

—— 1906. A contribution to the knowledge of the extinct avifauna of Australia. *Ann. Qd Mus.*, Brisbane, **6** : 1–25, pls 1–9.

FRAAS, O. 1870. Die Fauna von Steinheim. *Jh. Ver. vaterl. Naturk. Württ.*, Stuttgart, **26** : 281–283 ; pl. 13, figs 3a–c, 4.

LAMBRECHT, K. 1933. *Handbuch der Palaeornithologie.* xix + 1022 pp., 4 pls, 209 figs. Berlin.

LEAKEY, L. S. B. 1965. *Olduvai Gorge 1951–1961*, **1**. xiv + 118 pp., 97 pls, 2 figs, 1 map. Cambridge.

MILNE-EDWARDS, A. 1867. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*, **1** : 250–254 ; atlas **1** : pls 38–39. Paris.

WETMORE, A. 1933. Pliocene bird remains from Idaho. *Smithson. misc. Collns*, Washington, **87**, 20 : 1–12, 8 figs.

Widhalm, J. 1886. Die Fossilen Vogel-knochen der Odessaer Steppen-Kalk Stein-brüche der Neuen Slobodka bei Odessa. *Zap. novoross. Obshch. Estest.*, Odessa, **10**, Beilage: 4–6; pl. 5.

Dr C. J. O. Harrison, Ph.D.
Subdepartment of Ornithology
British Museum (Natural History)
Tring
Herts

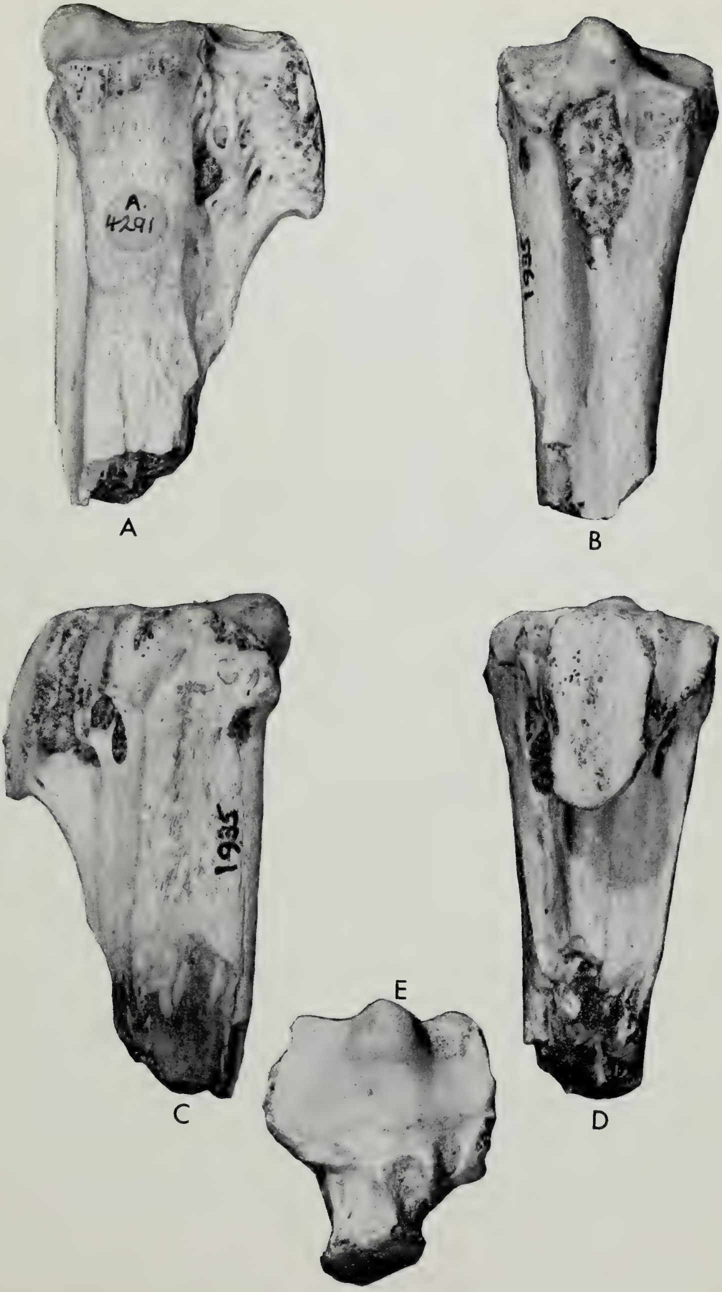
C. A. Walker
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Accepted for publication 9 February 1976

PLATE 7

Pelecanus aethiopicus sp. nov.

Holotype. Views of the proximal part of a right tarsometatarsus, BM(NH) No. A 4291. A, internal; B, anterior; C, external; D, posterior; E, proximal. × 1½.


A.
4291
A
1935
B
1935
C
E
D

CHELIDONOCEPHALUS TRILOBITE FAUNA FROM THE CAMBRIAN OF IRAN

By R. A. FORTEY & A. W. A. RUSHTON

ABSTRACT

A trilobite assemblage from the Mila Formation in northern Iran contains *Chelidonocephalus preannulatus* sp. nov., *Hadragnostus edax* sp. nov., *Koldiniella mitella* Sivov, *Peronopsis fallax* aff. *minor* (Brögger), *Dorypyge* sp., *Parakoldinia* ? sp. and *Tsinania* ? sp. It is of earliest Upper Cambrian age. The type species of *Chelidonocephalus* King (*C. alifrons*) and *Iranoleesia* King (*I. pisiformis*) are redescribed ; *Iranoleesia falconi* (King) is transferred to *Anomocarella.* Some problems in the classification of ptychoparioid trilobites are discussed.

INTRODUCTION

In NORTHERN IRAN Cambrian rocks crop out in the east–west trending Alborz Mountain belt south of the Caspian Sea. In western Iran further Cambrian outcrops are known along a belt parallel to the Zagros Thrust north-west of Shiraz (Fig. 12). Fossils from the latter area have been described by King (1937), and more recently Kushan (1973) described the faunas and zones of the Mila Formation (Stöcklin *et al.* 1964 : 20) in the Alborz Mountains.

While surveying the Qazvin quadrangle north-west of Tehran (Annells *et al.* 1975), Dr R. G. Davies collected fossiliferous samples from within *c.* 10 m of the local base of the Mila Formation near Sanghabad (field locality RD 569), at lat. 36° 06′ 43″ N, long. 50° 37′ 37″ E. These samples yielded an assemblage of trilobites somewhat ambiguous in age when compared with the faunas described by Kushan (1973). The assemblage includes well-preserved agnostids previously undescribed from Iran, and as a new species of *Chelidonocephalus* is present we have taken the opportunity to reassess *Chelidonocephalus* and associated genera and species known only from Iran, the affinities of which were obscure.

The trilobites are preserved, with fragments of horny brachiopods, in a grey sparry limestone cut by many minor joints. Several, but not all, show slight tectonic deformation. Although generally well preserved, the trilobites are all disarticulated and many were broken before fossilization.

Reference is made to specimens in the Palaeontology Department, British Museum (Natural History) (It and In), the Geological Survey of India (GSI) and the Institute of Geological Sciences, London.

We are grateful to Dr R. G. Davies for discussing the field occurrence of the fossils with us and to Mr S. F. Morris for technical assistance. A. W. A. Rushton publishes by permission of the Director, Institute of Geological Sciences.

Bull. Br. Mus. nat. Hist. (Geol.) **27**, 4 : 321–340 *Issued* 28 *October* 1976

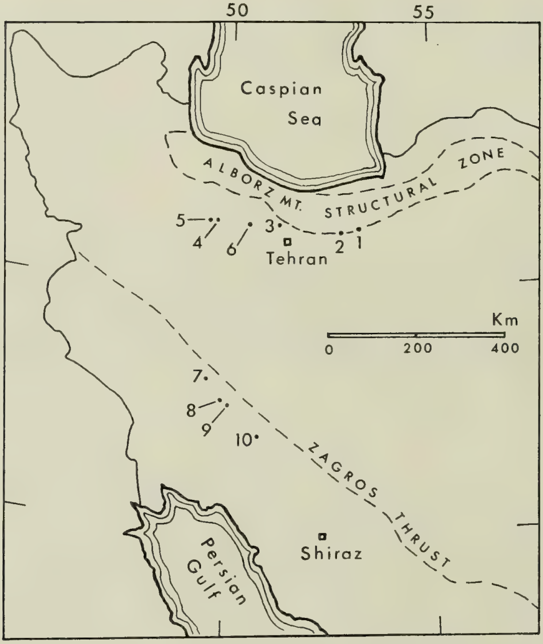


FIG. 12. Sketch-map of part of Iran. Structural lines from Stöcklin, 1968. Localities 1–5 are from Kushan 1973 : 1 = Mila Kuh, 2 = Shahmirzad, 3 = Haanakdar, 4 = Abhar, 5 = Qanli-Chapoghlu. Locality 6 = Sanghabad (R. G. Davies field Locality 569). Localities 7–10 are from King, 1937 : 7 = Chal-i-Sheh, 8 = Darreh Shu, 9 = Tang-i-Tehbud Bezuft, 10 = Ma'dan. *Chelidonocephalus alifrons* is recorded from localities 1, 3, 4, 5, 7, 8, 9, *Iranoleesia pisiformis* from 1, 3, 4, 5, 10 and *Koldiniella mitella* from 3, 4, 5, 6.

AGE AND CORRELATION OF THE FAUNA

Kushan (1973 : 125) recognized the following zones in the Mila Formation.

Tremadoc	*Saukia* Zone
Upper Cambrian	*Alborsella* Zone
	Kaolishania Zone
	Prochuangia Zone
	Drepanura Zone
Middle Cambrian	*Dorypyge* Zone
	Iranoleesia Zone

Iranoleesia is confined to its zone and is accompanied by *Anomocarella* etc. According to Kushan the several *Dorypyge* species are confined to the *Dorypyge* Zone and some are associated with agnostids and *Chelidonocephalus alifrons* or *C.* sp. The *Drepanura* Zone is characterized by *Drepanura* (*Spinopanura*) or by *Koldiniella*, or both, and also contains *C. alifrons*, *C.* sp. and agnostids. Kushan did not allow for an overlap of the ranges of *Dorypyge* and *Koldiniella*, such as occurs in the present assemblage.

We refer the present fauna to the *Drepanura* Zone because there are several specimens of *Koldiniella mitella* in the collection, and the presence of this species, of agnostids and of a species of *Chelidonocephalus* are typical of this zone. There is, on the other hand, only one specimen of *Dorypyge* and that is a different species from any recorded by Kushan from the *Dorypyge* Zone. On *a priori* grounds Kushan made a good case for the Middle Cambrian age of the *Dorypyge* Zone and the Upper Cambrian age of the *Drepanura* Zone, but as the new record implies an Upper Cambrian age for a *Dorypyge* species (a genus hitherto restricted to the Middle Cambrian) we here examine the age of the fauna in relation to the Middle–Upper Cambrian boundary. We accept the boundary as being between the *Lejopyge laevigata* Zone and the *Agnostus pisiformis* Zone, as reviewed by Daily & Jago (1975). *Chelidonocephalus* is restricted geographically and is of no help in wider correlation, nor is the *Tsinania* ? sp. because it cannot be convincingly compared with other described forms. *Peronopsis fallax* aff. *minor* resembles a subspecies known from the late Middle Cambrian of Scandinavia and *P. fallax* cf. *minor* from the *A. pisiformis* Zone in the Nuneaton district, England (Taylor & Rushton 1972 : 19). *Hadragnostus edax* sp. nov. is comparable with *H. las* Öpik from the *eretes* and *quasivespa* Zones of the Mindyallan Stage in Queensland : Öpik regarded these horizons as Upper Cambrian but Daily & Jago (1975 : 538) suggested that the *eretes* Zone and part of the *quasivespa* Zone should be correlated with the top of the *laevigata* Zone, thus making *H. las* a topmost Middle Cambrian species. A third species, *Hadragnostus modestus* (Lochman), occurs in the *Crepicephalus* Zone of Montana (Lochman 1944) in beds equivalent to part of the *A. pisiformis* Zone. Thus these agnostids do not give a precise age as they are related to forms occurring both above and below the Middle–Upper Cambrian boundary.

The only species of the present fauna found beyond the Mila Formation is *Koldiniella mitella* Sivov, which occurs in the lowest Upper Cambrian at Salair, western Siberia. Rozova (1968 : table 4) correlated this occurrence with the Kulyumbe 'superhorizon' of north-eastern Siberia which is referable to the *Pedinocephalina–Toxotis* (?) Zone, and this in turn was correlated with a level above the base of the *A. pisiformis* Zone by Daily & Jago (1975 : 546). *K. mitella* seems therefore to indicate an Upper Cambrian age, and with it goes the rest of the fauna, including the *Dorypyge* sp. We furthermore conclude that Kushan's choice of the Middle–Upper Cambrian boundary in the Mila Formation was apposite.

SYSTEMATIC DESCRIPTIONS

CLASSIFICATION PROBLEMS. One of the reasons palaeontologists find the mass of 'ptychoparioid' trilobites difficult to classify is that some persist in forcing genera into higher taxonomic groups on the basis of a single character in defiance of other characters which contradict such an assignment. Blindness and effacement of external features are thought to have been polyphyletically derived. Yet the blind

Conocoryphidae even now have the company of such distinct genera as *Hartshillia* and *Meneviella* thrust upon them despite Lake's observations that this ignores the characters of their thoraces and pygidia (1940 : 277). Similarly, Kobayashi, who recognized the polyphyletic character of effaced trilobites (1935 : 303), grouped nine varied genera in the Tsinaniidae (1960 : 397) but he himself regarded five of these as doubtful, with which we agree. We would add a sixth, *Koldinia*. This leaves the family with three closely related genera – *Tsinania*, *Dictyites* and perhaps the poorly known *Dictyella* : if Kobayashi is correct in regarding all these as effaced asaphiscids is there any need for a family Tsinaniidae at all?

We have considered the genera likely to be related to *Chelidonocephalus*, *Iranoleesia* and *Anomocarella* below without regard to the (apparently haphazard) arrangement of the families in which they have been included. This has not led to a satisfactory understanding of the families concerned, and we have therefore been forced to use the category 'family uncertain'.

Family **AGNOSTIDAE** McCoy 1849

Genus ***HADRAGNOSTUS*** Öpik 1967

Type species. Original designation, *H. las* Öpik 1967.

Discussion. *Hadragnostus* has a distinctive cephalon with a long glabella and short preglabellar field. The front of the cephalon is transverse and straight, or even slightly emarginate in *H. las* (Öpik 1967 : pl. 58, fig. 7) and *H. modestus* (Lochman 1944 : pl. 5, fig. 10) ; the new species *H. edax*, described below, has a straight or convex anterior margin.

The pygidium of *Hadrognastus* differs from that of *Peronopsis* in that it has a terminal node. *Baltagnostus* has a terminal node but the pygidial border between the posterolateral spines is widened medially (i.e. slightly crescent-shaped) or has a pygidial 'collar'. Öpik (1967 : 103) described the articulating device of *H. las* as simple, but the holotype of *H. edax* sp. nov. has an agnostoid articulation (Öpik 1967 : 72) which supports reference of *Hadragnostus* to the Agnostinae.

Hadragnostus edax sp. nov.

Pl. 11, figs 3–15

Derivation of name. Latin, *edax*, greedy, referring to the swollen pygidial axis.

Holotype. A well-preserved pygidium, It 13463 (Pl. 11, figs 7, 8, 12).

Type locality and horizon. Mila Formation, Sanghabad, Taleghan Range, Alborz Mountains, northern Iran.

Figured material. Cephala It 13468 (Pl. 11, fig. 3), It 13483a (Pl. 11, figs 9, 10), It 13483b (Pl. 11, figs 14, 15), It 14023 (Pl. 11, fig. 11). Pygidia It 13463 (holotype, Pl. 11, figs 7, 8, 12), It 13471 (Pl. 11, fig. 13), It 13472 (Pl. 11, figs 4–6).

Description. Cephalic outline tends to be subquadrate, length about four fifths of width. Glabella three quarters of cephalic length, bilobed; anterior lobe relatively small, nearly twice as wide as long, narrower than posterior lobe and one third of its length or less. Posterior lobe parallel-sided, rounded or slightly pointed behind, without lateral furrows or a median node, but some specimens have a faint posterior node (Pl. 11, fig. 15). Basal lobes triangular, inflated, connected behind glabella. Each cheek (excluding border) as wide as posterior glabellar lobe, tapering strongly forwards; in front of the glabella the cheeks are narrower than the length of the anterior glabellar lobe and are faintly separated by a partial preglabellar median furrow which forms a shallow depression just in front of the glabella and shallows or fades out forwards. Laterally and frontally the cheeks curve down steeply to the border which is mainly flat and horizontal but has a narrow outer rim and is curved under at the edge.

Thorax unknown.

Pygidium strongly convex, transverse, length about three quarters of width. Axis large, extending back to overhang the posterior border furrow. At anterior end axis is just less than half the total pygidial width, and widens slightly backwards. The articulating furrow has a depression either side of the median line, giving a weakly diplagnostid character. A median tubercle at the highest point has its posterior end just in front of the mid-length of the axis. Irregularities in the axial furrow indicate the merest traces of lateral furrows opposite the front and back of the median tubercle. A small terminal node lies well above the border furrow. Each flank about two fifths as wide as axis in the larger specimens but proportionally wider – nearly half the axial width – in a small specimen about 1·1 mm long. Flanks slope steeply down to the border, narrow backwards, separated behind axis. Border broad and thick, of even width between the small posterolateral marginal spines. Surface smooth.

Discussion. The present form is very similar to *Hadragnostus las* Öpik (1967 : pl. 58, figs 6–10) but has a slightly shorter and narrower anterior glabellar lobe. In *H. las* this lobe is more than one third of the length of the posterior lobe but in the present form it is less than a third. *H. las* has a stronger and wider preglabellar median furrow. The pygidial flanks are narrower, less than half the width of the axis, whereas in *H. las* they are more than half, and in Öpik's reconstruction (1967 : 103, text-fig. 24) the posterolateral marginal spines are shown as larger than those of *H. edax*.

One figured cephalon of *Hadragnostus modestus* (Lochman 1944 : pl. 5, fig. 10) is typical of the genus: the anterior glabellar lobe is narrower than the posterior lobe but it is longer than in *H. edax*. The preglabellar median furrow is narrower than that of *H. las* and stronger than in *H. edax*. The basal lobes of *H. modestus* are smaller than in either of the other species. Lochman's other figured cephalon has a more rounded outline, the posterior glabellar lobe is more tapered and the preglabellar field is longer; it may represent another genus. The holotype and paratype pygidia of *H. modestus* are meraspids with the median tubercle at the mid-length of the pygidium. Full comparison with *H. edax* cannot be made.

Family **QUADRAGNOSTIDAE** Howell 1935

Genus ***PERONOPSIS*** Hawle & Corda 1847

Type species. By monotypy, *Battus integer* Beyrich 1845.

Peronopsis fallax (Linnarsson 1869) aff. ***minor*** (Brögger 1878)

Pl. 12, figs 1–14

Figured material. Cephala It 13480a–b (Pl. 12, figs 1, 2), It 13480c (Pl. 12, figs 3, 4), It 13480d (Pl. 12, fig. 14), It 14024 (Pl. 12, figs 9, 11), It 14026 (Pl. 12, fig. 10). Pygidia It 13467 (Pl. 12, fig. 6), It 13469 (Pl. 12, figs 12, 13), It 13485 (Pl. 12, figs 5, 8), It 14025 (Pl. 12, fig. 7). Some twenty unfigured cephala and pygidia also present.

Description. Cephalon rounded in front, nearly as long as wide. Glabella about 0·7 of cephalic length, bilobed; anterior lobe rounded in front, slightly narrower than, and less than two fifths the length of, the posterior lobe. Transglabellar furrow narrow at external surface, broader in exfoliated specimens. Posterior glabellar lobe has faint lateral furrows at two fifths of its length from the front and a faint median node, generally elongate, at or in front of its mid-length; bluntly rounded behind. Basal lobes triangular but with a forward extension in some specimens which indents the sides of the glabella, somewhat as in *Ptychagnostus atavus* (Tullberg); this feature is not seen in exfoliated specimens. Cheeks about as wide as glabella, narrowing forwards slightly, confluent in front. A pit resembling an incipient preglabellar median furrow is seen in front of the glabella in some specimens. Cheeks slope steeply down to border in small or exfoliated specimens, less steeply in the largest specimens. Border furrow is a curve where the cheeks flatten out to form a border, and is broad in large specimens. Border is a narrow convex rim.

Thorax unknown.

Pygidium convex, subquadrate, length about 0·9 of width. Axis about two fifths of total width, parallel-sided with a tendency to narrow slightly at the anterior third. Posterior end generally bluntly pointed but may be rounded, especially in large specimens, not reaching border. Median tubercle at anterior two fifths; traces of lateral furrows opposite anterior and posterior ends of tubercle. Articulating device simple, basic (Öpik 1967 : 72). Flanks (pleural lobes excluding border) about half the width of axis but proportionally narrower in specimens more than 2 mm long, and always confluent behind axis although the connection is narrow in some specimens. Border furrow broad and shallow. Border broad, of even width between the strong posterolateral marginal spines. Surface smooth.

Discussion. In most features the present form falls within the wide range shown by Westergård's (1946 : pl. 3, figs 3–7) figures of *P. fallax minor*. It differs from many *Peronopsis* species in that the pygidial flanks are confluent behind the axis, and resembles *P. fallax minor* but not *P. fallax ferox* (Tullberg) in the character of the cephalic border (Westergård 1946 : 38). The cephala agree with Westergård's figures although the glabella is generally longer than in his fig. 4 and the anterior glabellar lobe is proportionally longer than in his fig. 3; neither figure shows a preglabellar depression or elongated *Ptychagnostus*-like basal lobes. A specimen of *P. fallax* cf. *minor* (Pl. 12, fig. 15) from the *A. pisiformis* Zone of central England (Taylor & Rushton 1972 : 19) has a weak preglabellar depression but differs in having a longer anterior glabellar lobe and smaller basal lobes; the pygidial axis is evenly rounded behind. Probably compression has caused the lateral margins of the pygidium to converge backwards slightly.

Some of the pygidia of '*Agnostus*' *simplexiformis* Rozova (1964 : 24) resemble that of the present form. Rozova figured no cephala of '*A.*' *simplexiformis* but Lazarenko & Nikiforov (1968 : pl. 3, figs 1–4) showed that both cephalon and pygidium have constricted acrolobes (Öpik 1967 : 68). Judging from these figures we would transfer '*A.*' *simplexiformis* to *Agnostoglossa* Öpik (1967 : 145).

Family **DORYPYGIDAE** Kobayashi 1935

Genus ***DORYPYGE*** Dames 1883

TYPE SPECIES. Original designation, *Dorypyge richthofeni* Dames 1883.

DISCUSSION. About forty specific names have been applied to *Dorypyge, sensu stricto*, but according to Kobayashi's revision (1960 : 347) many of these are synonyms. Kushan (1973) has discussed six forms from Iran.

Dorypyge sp.

Pl. 11, figs 1, 2

MATERIAL. One fragmentary pygidium about 7 mm long, It 13461.

DESCRIPTION. Outline, excluding spines, trapezoidal, width nearly 1·5 times length. Axis only slightly tapered backwards, composed of three well-defined rings, a fourth less well defined, and a rounded bulbous terminal part. Flanks slightly narrower than axis anteriorly, marked by three pairs of narrow pleural furrows but no interpleural grooves. Border broad, the anterior pleural furrows crossing it indistinctly. Medially, the border forms a narrow transverse connection behind the axis. Convex parts of surface covered with sparse coarse granules. The marginal spines are distinctive although not all are preserved. The pygidium follows the common plan of *Dorypyge* species in having four pairs of main marginal spines anterior to the largest pair, but the present form is unusual, and perhaps unique, in showing a small subsidiary spine anterior to each of the first three of the 'main' spines; their bases make the outline of the pygidium jagged. Whereas the thickness of the 'main' spines increases from the first to fourth pair, the subsidiary spines are progressively thinner from the first to third pair. The fifth pair of marginal spines is represented only on the left by a scar where the spine is broken off; it was twice as thick as the fourth spine. The outline of the posterior part of the pygidium suggests the former presence of a substantial sixth pair of spines. The doublure, which is partly exposed, is a smooth band parallel to the margin and convex ventrally.

Discussion. The present form differs from all species so far described in having subsidiary pygidial spines. However Dr P. Jell has told us of certain *Kootenia* species which also show 'subsidiary' marginal spines which point more nearly ventrally and are correspondingly difficult to observe. Their presence suggests that similar spines may be found in other Dorypygidae. In other respects the present form resembles the subspecies *D. richthofeni laiwuensis* Kobayashi, which lacks interpleural grooves, and the form figured by Sun (1924 : pl. 2, figs 3 c, d) which Kobayashi (1960 : 348) referred to *D. r. laevis*. Sun's fig. 3d shows that the marginal spines increase in size backwards and also shows sparse granulation, but it differs in having slightly wider flanks and only three axial rings. The present specimen is distinguished from *D. iranensis* Kushan and *D. khademi khademi* Kushan by the granular surface, and from *D. khademi papillosa* Kushan by the absence of interpleural grooves. The fragment illustrated by Kushan (1973 : pl. 28, fig. 8) as *D. richthofeni* n. subsp. aff. *richthofeni* differs slightly in having wider axial ring furrows and pleural grooves, and a wider (sag.) post-axial part of the border.

Family **ASAPHISCIDAE** Raymond 1924

Genus ***IRANOLEESIA*** King 1955

(*Pro Irania* King 1937, *non* De Filippi 1863)

Diagnosis. Asaphiscid trilobites with glabella slightly tapering, truncate anteriorly. Posterior two pairs of glabellar furrows deep, inner half of 1P bifurcate, posterior branch directed obliquely backwards. Occipital ring may be subdivided with lateral lobes. Postocular fixed cheeks small (sag., trans.).

Type species. Original designation, *Irania pisiformis* King 1937.

Discussion. The type species (and, with the removal from *Iranoleesia* of *Irania falconi* King 1937, the only species) of *Iranoleesia* is redescribed below. Kobayashi (1967 : 439) indicated that *Iranoleesia* may be a junior synonym of *Hundwarella* Reed 1934, from the Cambrian of Kashmir. The two specimens on which the type and only species of *Hundwarella* is based, both cranidia, show apparently bifurcate inner ends of the 1P glabellar furrows (Reed 1934 : pl. II, figs 5, 6) which connect across the middle of the glabella. This is not the case in *Iranoleesia pisiformis*, but the Kashmir specimens are slightly crushed, and the apparent transverse furrows may be the result of compressing bifurcate furrows of *Iranoleesia* type. A similar effect may be observed on flattened specimens of *Hypermecaspis* (compare Fortey 1974 : pl. 13, fig. 1 with Lake 1913 : pl. 7, fig. 3). Even if this is accepted *Iranoleesia pisiformis* differs from *Hundwarella* in having a transversely truncate front margin of the glabella, the preglabellar field only half as wide (sag.), and a strongly punctate surface sculpture. Since the significance of such characters in discriminating asaphiscid genera is still imperfectly appreciated, *Iranoleesia* is therefore retained here pending a revision of the whole group. For example, the genus *Iniotoma* Öpik 1967, from the Mindyallan, has apparently similar glabellar furrows (Öpik 1967 : 232, fig. 81) to those of *Iranoleesia*, but they are less impressed and the eye ridges are less distinct (1967 : pl. 11, figs 1–3). While it seems probable that these genera are separated more by geography than by morphology, a revision of the genera is beyond the scope of the present account. The genus *Protohedinia* Endo 1937 (the type species of which has been illustrated by Chang 1963 : pl. 1, fig. 9) has glabellar furrows similar to those of *Iranoleesia* and has palpebral lobes similarly placed, eye ridges of like prominence, and border and preglabellar fields of similar proportions. It is difficult to see why it has been included in a separate family Tengfengiidae by Chang (1963 : 458).

Iranoleesia pisiformis (King 1937)

Pl. 9, figs 6, 8–10, 12

1937 *Irania pisiformis* King : 12–13 ; pl. II, figs 6a–c

DIAGNOSIS. *Iranoleesia* species with pitted surface sculpture. Anterolateral corners of glabella angulate. Anterior border furrow without plectrum.

HOLOTYPE. Although not named as such, it is clear from the plate description and measurements given by King (1937 : 13 ; pl. II, fig. 6) that he intended the incomplete cranidium, GSI 16305, as holotype of this species. We figure a cast of this original on Pl. 9, fig. 6.

TYPE LOCALITY AND HORIZON. Ma'dan, locality 12 of King (1937). The exact stratigraphic relationship of this species to the new *Chelidonocephalus* fauna is not known for certain but Kushan recorded *I. pisiformis* only from horizons below those with *Koldiniella mitella*, suggesting that the *Chelidonocephalus* fauna is slightly the younger.

FIGURED MATERIAL. Cranidia In 36890 (cast of holotype, Pl. 9, fig. 6), In 36910 (Pl. 9, fig. 8), In 36911 (Pl. 9, fig. 10), In 36912 (Pl. 9, figs 9, 12).

DESCRIPTION. Only cranidia known with certainty, and available material largely decorticated, but otherwise well preserved in a limestone matrix. General cranidial outline subquadrate, with anterior margin not greatly protruded, glabella but slightly elevated above fixed cheeks, sloping downwards anteriorly into preglabellar field. Glabella (with occipital ring) almost rectangular, extending to three quarters cranidial length, tapering very gently forwards, so that the axial furrows enclose an angle of about 15°. Anterolateral corners of the glabella are obtusely angulate, resulting in a truncate anterior glabellar margin. Four pairs of lateral glabellar furrows, of which the anterior two pairs are shallow and probably would not be visible on the dorsal surface of the cuticle. 1P has its outer end opposite the midpoint of the palpebral lobe, its outer third running transversely or slightly posteriorly, at which point it bifurcates into a short, slightly anteriorly-directed branch, and a longer, strongly backward-directed posterior branch, the inner end of which terminates at about one third glabellar length. 2P, with its outer end almost opposite the front of the palpebral lobe, is arcuate, the inner end curving backwards in line with the inner end of 1P. 3P and 4P opposite the eye ridge, the former isolated within the glabella, transverse, the latter short, slightly forward-inclined, placed laterally to 3P. Occipital furrow deep, forward-curved medially, and shallowing laterally ; occipital ring with indistinctly defined lateral lobes and prominent median tubercle. Axial furrows distinct, as is the preglabellar furrow on the smaller cranidium (Pl. 9, fig. 8), although on larger specimens this furrow becomes shallower to almost effaced medially.

Intraocular fixed cheeks about half width (trans.) of adjacent glabella, horizontal. Preglabellar field about one sixth length of glabella (sag.), scarcely downsloping medially ; that part of the fixed cheeks in front of the eye ridge slopes downwards more steeply and is about twice the length (exsag.) of the preglabellar field (seen in dorsal view). The eye ridges are strong on internal moulds, converging forwards at about 65° to the sagittal line. Palpebral lobes of about same width as the eye ridges, in a posterior position such that the transverse line connecting their anterior limits crosses the glabella at two thirds its length ; they are of length (exsag.) one third, or slightly less, that of glabella. Anterior border furrow defining change in slope from preglabellar field to broad, backward-sloping anterior border, the width of which (sag., exsag.) is similar to that of the preglabellar field. Postocular cheeks poorly shown by present material.

Genus ***ANOMOCARELLA*** Walcott 1905

DIAGNOSIS. Asaphiscid trilobites with glabellar furrows faint or absent ; preglabellar field less than one fifth glabellar length ; anterior border furrow with narrow (trans.) plectrum ; anterior border flat. Pygidium with distinct flat border.

TYPE SPECIES. Original designation, *Anomocarella chinensis* Walcott 1905.

DISCUSSION. The species described below as *Anomocarella falconi* was originally assigned to *Irania* by King (1937), and hence subsequently to *Iranoleesia*. Kobayashi (1967 : 493) preferred to regard the species as belonging to *Grandioculus* Cossmann. The type species of that genus, *G. megalurus* (Dames) (Dames 1883 : 20 ; pl. 1, figs 7, 8, 10. Walcott 1913 : 192 ; pl. 18, figs 9a–f) has large, somewhat posteriorly placed palpebral lobes, weakly defined glabellar furrows and a flat border like that of the Iranian specimens, but the border furrow lacks a plectrum, which is also the case in *Iranoleesia pisiformis*. The type species of *Anomocarella* is *A. chinensis* Walcott 1905, the lectotype of which was carefully identified by Endo & Resser (1937 : 164–165). This cranidium is only one of the specimens used by Walcott (1913 : pl. 20, figs 3, 3a–d, 4, 4a) to illustrate *A. chinensis*, and all the others are from a different locality from the lectotype (pl. 20, fig. 3c) and include more than one species (Endo & Resser 1937 : 165). It is the other material (the specimens of Walcott 1913 : pl. 20, figs 3, 3e) that is used to illustrate the type species of *Anomocarella* in the Treatise (Howell *in* Harrington *et al.* 1959 : 292). Endo & Resser emphasized the presence of a plectrum as 'the most distinctive generic feature' of *Anomocarella*, with which we agree. The major point of difference between the Iranian material and the type species is the shorter preglabellar field of the latter ; this is not regarded as of generic importance, as it is a variable feature in other species assigned to *Anomocarella* by Endo & Resser (1937). Further backward migration of the plectrum (or further shortening of the preglabellar field) results in the broadly backward-deflected border furrows seen in *Mapania* (Öpik 1961 : fig. 53).

Anomocarella and allied genera are sometimes referred to a separate family Anomocarellidae Hupé 1955. Since the characters pertinent to the division of genera within the Asaphiscidae and *Anomocarella*-group are unclear at best, and there is no phyletic concept on which to base separate families, *Anomocarella* is here retained doubtfully within the Asaphiscidae.

Anomocarella falconi (King 1937)

Pl. 9, fig. 11 ? ; Pl. 10, figs 1–5, 8

1937 *Irania falconi* King : 13–14 ; pl. II, figs 7a–f.

DIAGNOSIS. An *Anomocarella* species with transverse width of plectrum half to two thirds that of anterior margin of glabella ; preglabellar field of moderate width ; dorsal surface of cuticle minutely granulose.

HOLOTYPE. An external mould of a cranidium, a cast from which was figured by King (1937 : pl. II, fig. 7a), GSI 16306. This cast is here refigured on Pl. 10, fig. 1.

TYPE LOCALITY AND HORIZON. Mila Formation at Darreh Shu (lowest beds), locality 8 of King (1937), whence *Chelidonocephalus alifrons* is also recorded (King 1937 : 17).

FIGURED MATERIAL. Cranidia In 36891 (cast of holotype, Pl. 10, fig. 1), In 36908 (Pl. 10, fig. 3), In 36909a (Pl. 10, fig. 2), In 36909b (Pl. 10, figs 4, 5, 8). Doubtfully assigned pygidium In 36892 (cast, Pl. 9, fig. 11).

DESCRIPTION. Cranidium of low convexity, downward-sloping in front of eye ridges, glabella not greatly vaulted above intraocular cheeks. Maximum cranidial width at posterior margin about one and a half times transverse width at anterior border. Glabella extends to about three quarters cranidial length, and tapers uniformly forwards, the axial furrows enclosing an angle between 15° and 20°. Anterolateral corners of glabella rounded ; axial furrow deeper than preglabellar furrow, and both better defined on internal moulds. Occipital and glabellar furrows faint, best seen as smooth, slightly depressed areas on specimen retaining exoskeleton (Pl. 10, fig. 8). 1P to 3P almost touch axial furrows ; distance (exsag.) between 1P and 2P equal to that between 1P and the occipital furrow, but less than that between 2P and 3P ; 3P is level with the point at which the eye ridges touch the glabella, transverse ; 1P and 2P slope slightly backwards. 4P is very close to 3P but external to it, continuing in line with the furrow defining the posterior of the eye ridge. Occipital ring widest (sag.) medially, defined by broad, shallow furrow, of which only the transverse, median section is visible on the internal mould (Pl. 10, fig. 3) ; outer ends of this section deepened into internal muscle scars. External surface shows narrow parafrontal band in front of midpart of frontal glabellar lobe ; this band extends further laterally on the internal mould, but neither on dorsal nor on ventral surfaces is the connection with the eye ridge displayed.

Palpebral lobes of half length of glabella, anterior limit opposite outer ends of 3P furrows ; palpebral rims broad, defined by shallow palpebral furrows which are outward-bowed medially. Maximum transverse width of intraocular cheek half width of adjacent glabella. Eye ridges not visible abaxially on dorsal surface of exoskeleton, but their confluence with the frontal lobe of the glabella is clearly shown by anterior shallowing of the axial furrows. The eye ridges, where seen, are only slightly oblique, virtually transverse on the smallest cranidium. Postocular fixed cheeks narrow, width (exsag.) less than that of occipital ring, bisected by strong border furrow. Narrow posterior border carries small articulating socket (?) at about mid-width, maximum transverse width of border less than that of occipital ring. Preglabellar field of length (sag.) between 0·14 and 0·17 times glabellar length on available material. Anterior border furrow marks an abrupt change in slope anterolaterally, where it is gently bowed forwards ; medially there is a distinct plectrum, of transverse width about half to two thirds that of frontal lobe of glabella. Laterally the wide anterior border is horizontal to slightly declined, but in front of the plectrum more nearly carries forwards the downward slope of the preglabellar field. There are faint indications of caeca crossing the border furrow. The dorsal surface of the exoskeleton is covered with minute granules.

An incomplete pygidium (Pl. 9, fig. 11) was assigned to this species by King (1937 : pl. II, fig. 7b). It has a convex rhachis showing three or four axial rings and a broad flattened border. It also resembles the posterior part of the pygidium here tentatively assigned to *Chelidonocephalus preannulatus* sp. nov. (p. 338), and it must be admitted as a possibility that the pygidium is that of *C. alifrons*. Our material is inadequate to resolve the question.

DISCUSSION. *Anomocarella falconi* differs from the type species *A. chinensis* (Walcott 1913 : pl. 20, fig. 3c. Endo & Resser 1937 : pl. 34, fig. 6) in having less oblique eye ridges (due to an anterior forward limit of the palpebral lobe) and a longer (sag., exsag.) preglabellar field ; the surface sculpture of *A. chinensis* is described as punctate. Of the many species assigned by Walcott (1913 ; some re-illustrated in Lu *et al.* 1965 : pls 59–61) to *Anomocarella* only the type species has a plectrum, and the others should be excluded from the genus. One of the species from the Mapan Formation, *A. concava* Endo & Resser (1937 : 167 ; pl. 35, fig. 8), approaches *A. falconi* closely in the proportions of preglabellar field and plectrum. It differs only in having a glabella that hardly tapers forwards, and anterior limits of the palpebral lobes that approach the glabella more closely.

Genus ***KOLDINIELLA*** Sivov 1955

TYPE SPECIES. Original designation, *K. mitella* Sivov 1955.

DISCUSSION. This genus is characterized by a broad, flat cephalic border and effacement of the other cephalic characters. Traces of the axial furrow suggest that the glabella extends to or nearly to the anterior border (Kushan 1973 : pl. 31, fig. 3) ; this feature, the more backward eyes and the transverse pygidium distinguish *Koldiniella* from the more effaced forms of *Maryvillia* and *Blountia* (Rasetti 1965 :

pls 9, 10). *Koldiniella* is similar to but more effaced than the asaphiscid *Peishania* Resser & Endo from the late Middle Cambrian ; it may even have been derived from a form like *P. lubrica* Chang (1957 : pl. 1, fig. 2) which has a comparable frontal border but has the axial furrows and occipital furrow more distinct. *Peishania* (and *Liopeishania* Chang 1963, to which *P. lubrica* was transferred in Lu *et al.* 1965) have longer pygidia than *Koldiniella mitella.* The dorsal surface of the cranidium of *Liopeishania spannensis* Palmer & Gatehouse is more effaced than other species and approaches *Koldiniella* in this respect. It differs in having a shorter anterior border which is curled down and under in front (Palmer & Gatehouse 1972 : pl. 4, fig. 10).

Koldiniella has been variously grouped with the families Illaenidae, Illaenuridae and Tsinaniidae on account of its effaced cephalon, but there are no characters uniting it convincingly with any of these families and the frontal border is a feature distinguishing it from all (and from *Kingstonia*). It perhaps comes closest to the Illaenuridae because *Illaenurus* has a transverse pygidium and in *Macelloura* the glabella reaches to the frontal border.

Koldiniella mitella Sivov 1955

Pl. 10, figs 6, 7, 9, 10, 15, 13 ?, 14 ?, 16 ?

FIGURED MATERIAL. Cranidium It 14021 (Pl. 10, figs 6, 7) ; pygidia It 13477 (Pl. 10, figs 9, 10), It 14022 (Pl. 10, fig. 15) ; hypostome assigned to the species It 13506 (Pl. 10, fig. 16) ; cranidium doubtfully assigned, It 13476 (Pl. 10, figs 13, 14). Ten unfigured specimens also present.

DISCUSSION. Kushan (1973 : 149) redescribed this species using material from Iran. Material in the present collection is identical. A hypostome tentatively referred to *K. mitella* (Pl. 10, fig. 16) has a gently convex median body divided by a faint transverse furrow. The lateral border widens out posterolaterally but is narrow posteromedially. The surface is smooth except posterolaterally where it is striated parallel to the margin. This hypostome cannot be that of *Dorypyge* because it differs from that referred to *Dorypyge aenigma* (Westergård 1948 : pl. 2, fig. 7) ; the smooth surface and striated margin recall *Koldiniella mitella* rather than the associated *Chelidonocephalus preannulatus.*

K. mitella is distinguished from *K. convexa* Lazarenko by the longer and flatter anterior border and by the weaker axial furrows at the base of the glabella (Rozova 1964 : pl. 15, figs 1–5).

K. prolixa Lazarenko (*in* Lazarenko & Nikiforov 1968 : pl. 1, figs 16–19) has a longer, more salient frontal border and a much longer pygidium, nearly as long as wide.

One small cranidium 1·7 mm long (Pl. 10, figs 13, 14) has a much narrower (sag.) frontal border, less than a tenth of the length of the cranidium. It may possibly be a juvenile form of *K. mitella* because among larger specimens the border seems to have grown more rapidly than the rest of the cranidium, but the border is convex instead of being flat or even slightly concave as it is in specimens of *K. mitella* 3 mm or more in length. The small cranidium may therefore be referable to *Parakoldinia* Rozova

1960. It is most closely comparable with *P. plana* Rozova (1960 : pl. 7, figs 1–5), a broad and not especially convex species with a distinct frontal border, horizontal in front view, which does not show strong striae. Unfortunately the present specimen is too different in size for an exact comparison to be made, but Rozova's fig. 3 shows the border furrow more sharply cut and the border dropping abruptly downwards in front, whereas in the present specimen the border curves down more gradually in front.

Genus ***TSINANIA*** Walcott 1914

Type species. Original designation, *Illaenurus canens* Walcott 1905.

Discussion. Kobayashi (1935 : 303) has suggested that *Tsinania* is an effaced member of the Asaphiscidae.

Tsinania ? sp.

Pl. 10, figs 11, 12, 17–19

Figured material. Cranidia It 13493 (Pl. 10, figs 11, 12), It 13458 (Pl. 10, figs 17–19).

Description. Cranidium convex. Axial furrows effaced at external surface but a trace of their ends seen on the exfoliated specimen. The base of the glabella is a little more than half as wide as the cranidium. No trace of occipital or glabellar furrows. In palpebral view the middle of the eyes lies just behind the mid-length. Palpebral furrow very faint. Preocular sutures diverge forwards slightly but curve inwards across the anterior border. Postocular sutures diverge backwards obliquely, straight. A very faint border furrow separates off a narrow, barely differentiated frontal border. Pleuroccipital furrow weak. Surface smooth.

Discussion. These specimens agree closely with *Tsinania canens* (Walcott 1913 : pl. 23, fig. 2) except that the eyes seem farther forward, the base of the glabella is wider and there is a very faintly marked border. Kobayashi (1952) revised *Tsinania canens* and showed that the glabella is less than half as wide as the cranidium. No published figures show a frontal border. *Tsinania* ? sp. also resembles *Plethometopus obtusus* Rasetti (Longacre 1970 : pl. 6, figs 14, 15) except that the latter has a well-marked occipital furrow and curved postocular sutures. *Plethometopus convergens* (Raymond) has only a weak occipital furrow but the preocular sutures converge forwards (Longacre 1970 : pl. 3, figs 11, 12). *Plethopeltoides lepidus* Lazarenko (*in* Lazarenko & Nikiforov 1968 : pl. 9, figs 1–7) has a better-marked occipital furrow and is less convex. *Wanwanoglobus convexus* (Kobayashi 1966 : 265 and text-fig. 4) has a much more convex cranidium. We know of no Cambrian trilobite which matches the present cranidium in all details.

Family **UNCERTAIN**

Genus ***CHELIDONOCEPHALUS*** King 1937

Diagnosis. Cranidium opisthoparian, 'ptychoparioid', with glabellar furrows (other than occipital) not incised. Broad false border furrow delimiting flattened or gently convex anterior cranidial border. True border furrow crosses preocular cheek, cut by preocular suture at sutural mid-length (exsag.), inner ends of border furrow curve backwards to define the plectrum. Narrow (sag.), transverse inflated band in front of glabella. Broad palpebral lobes between one third and half glabellar length, posterior limits opposite outer parts of occipital furrow defining narrow (exsag.) postocular cheek. Width of intraocular cheek less than that of adjacent glabella. Eye ridges subdued.

Type species. Original designation, *C. alifrons* King 1937.

Discussion. *Chelidonocephalus* was placed in the Alokistocaridae in the Treatise (Howell *in* Harrington *et al.* 1959 : 238), but other possibilities must now be considered. Chang (1959 : 223) allied *Chelidonocephalus* with a number of Middle Cambrian genera from China, including *Poshania* Chang 1957 (type species *P. poshanensis* Chang 1957), *Peichishania* Chang 1957 (type species *Eymekops rectangularis* Endo & Resser 1937), *Inouyella* (type species *I. peiensis* Endo & Resser 1937), *Ordosia* (type species *O. fimbricauda* Lu 1954) and *Taitzuia* (type species *T. insueta* Endo & Resser 1937). All these genera share with *Chelidonocephalus* the backward-curved border furrow (termed below the 'true' border furrow), although the development of the border itself is variable. In the Treatise (Harrington *et al.* 1959) *Chelidonocephalus, Ordosia, Inouyella* and *Taitzuia* are assigned to four different superfamilies, while Chang (1959 : 223) indicates that they may be included within a single family Namanoiidae Lermontova 1951, based on the Lower Cambrian genus *Namanoia* from eastern Siberia, which has a similar disposition of furrows on the cranidial margin. We believe that the form of the border furrows is assuredly significant at generic level, but that its significance at family level is more contentious. The backward-curving border furrows are present, for example, on *Llanoaspis walcotti* Resser (Rasetti 1965 : pl. 8, fig. 14) from the Upper Cambrian of Tennessee, which is certainly unrelated to *Chelidonocephalus* and the other genera listed above, having distinctively different facial sutures. Similarly *Namanoia*, with its quadrate glabella and lack of parafrontal band, is unlikely to be closely related to *Chelidonocephalus*, which therefore cannot be assigned to the Namanoiidae.

We consider that *Chelidonocephalus* is most nearly related to *Poshania*, which is identical in the combination of true border furrow and parafrontal band (Chang 1959 : pl. 2, figs 4, 5), and differs significantly only in lacking a distinct false border furrow. The resemblance is perhaps more apparent when comparing small cranidia of *Chelidonocephalus* (Pl. 9, fig. 5) with adult *Poshania* as the whole border region is then of similar proportions. *Peichishania, Inouyella, Ordosia* and *Taitzuia* are probably unrelated to these two genera ; *Peichishania* was assigned by Öpik (1967 : 221) to the Auritamidae, *Ordosia* by Lu (1954) to the Leiostegiidae (and *Taitzuia* closely resembles *Ordosia*). *Inouyella*, with its tapering glabella with narrow, backward-directed furrows (Endo & Resser 1937 : pl. 46, figs 9, 14), is probably unrelated to any of the foregoing.

The Alokistocaridae have been included within the concept of the Papyriaspididae by Öpik (1961 : 149). He (Öpik 1967 : 298) includes *Poshania* (misspelt *Poshauia*) in the family Mapaniidae of his superfamily Rhyssometopacea, which might therefore be expected to include *Chelidonocephalus* also. We briefly discuss below (p. 337) some reasons for treating a rhyssometopacean affinity with caution.

This discussion shows to what an extent the familial (and superfamilial) concepts are capable of varied interpretations in these late Middle to early Upper Cambrian forms. For the time being, therefore, we have to leave *Chelidonocephalus* as of uncertain family.

Chelidonocephalus alifrons King 1937

Pl. 8, figs 1–5

DIAGNOSIS. *Chelidonocephalus* species with punctate surface sculpture. Anterior border of cranidium gently convex. Palpebral lobes farther from glabella, and convexity lower than that of *C. preannulatus* nov. sp. (p. 338).

LECTOTYPE. King (1937) did not specify a holotype for this species, but of his original syntypic series that figured in his pl. II, fig. 8A corresponds with the measurements cited in the text, and was probably intended as the type. We therefore select this specimen, GSI 16311, as lectotype.

TYPE LOCALITY AND HORIZON. The lectotype is associated with *Anomocarella falconi* (King) from a limestone 2300 feet (700 m) below the local top of the Cambrian, at Chal-i-Sheh (loc. 3 of King 1937 : text-fig. 1). The evidence from Kushan's (1973) faunal lists with *Chelidonocephalus* is that a late Middle Cambrian or an earliest Upper Cambrian age is most probable for these beds.

FIGURED MATERIAL. Cranidia In 36893 (cast of lectotype, Pl. 8, fig. 1), In 36895 (Pl. 8, figs 2, 3, 5), In 36896 (Pl. 8, fig. 4).

DESCRIPTION. Cranidia only identified with certainty, these being well preserved in limestone. Convexity is low, the whole surface of the cranidium sloping gently downwards and forwards from the occipital ring. The largest specimen, a fragmentary cranidium, probably had a cephalic length of about 20 mm. Maximum transverse width, across posterior margin, about one and a half times the width across the anterior cranidial margin. Glabella tapering gently forwards, axial furrows enclosing an angle of about 30°, extending to about 0·7 of the cranidial length (sag.) ; front margin truncate. Glabellar furrows absent, but muscle insertion areas are represented by smooth areas lacking the pitted sculpture which covers the rest of the glabella. There is a pair of large smooth areas centred on the lateral parts of the occipital furrow, and three (? four) pairs of ill-defined smooth areas on the flanks of the glabella. The occipital furrow is shallow except where deepened into pits near its lateral extremities. Postocular and preocular fixed cheeks downsloping ; intraocular cheek horizontal. Palpebral lobes about one third glabellar length, with posterior limits slightly in front of points at which the occipital furrow meets the axial furrows. Transverse width of the intraocular cheek at anterior limit of palpebral lobe is about 0·7 of the width of glabella at same section. Palpebral furrows are faint even on internal moulds. Eye ridges are faint on the external surface of the cuticle, but clearly visible on internal moulds (Pl. 8, fig. 4); their adaxial limits indent the course of the axial furrows. Posterior border furrow deep and transverse; convex posterior border of width (exsag.) subequal to that of furrow. In front of the glabella there is a narrow (sag., exsag.) transverse inflated band, defined posteriorly by the preglabellar furrow and anteriorly by the true anterior cranidial border furrow. This latter follows a transverse, gently curved course a little anterior to the front margin of the glabella, medially deflected sharply backwards when approaching the anterolateral corners of the glabella, to form the median plectrum (Öpik 1967 : 58), this area being inflated above the genal areas adjacent to it. The anterior border furrow is cut by the anterior branch of the facial suture at, or slightly in front of, the anterior sutural mid-length. In front of the plectrum the preglabellar field continues a gently downward slope into a broad, shallow false border furrow. The gently convex anterior border widens medially, where it occupies one third to one quarter of the total preglabellar length. Internal moulds are strongly caecate on frontal part of cranidium; caeca pass over both border furrows, but are not visible behind eye ridge. Dorsal surface of cranidium is finely pitted except in furrows and over muscle insertion areas. In front of the true border furrow, the pits are replaced by more densely crowded, minute granules.

Discussion. The description of 'true' and 'false' border furrows used above needs clarification. It is contended that the posterior of the two transverse furrows crossing the preglabellar area represents the border furrow as understood in other trilobites, and that the anterior furrow in *Chelidonocephalus* is independently generated. Homologically, all that area anterior to the true border furrow should be termed 'anterior border', but for convenience the area is divided into preglabellar field, 'false' border furrow and anterior border in line with other trilobites. The identification of the posterior of the two furrows with the anterior border furrow of other trilobites is based on the fact that this furrow has a median plectrum, and that the plectrum is invariably developed on the anterior border furrow. Since plectra are developed in a number of groups which are, at least on present classifications, only distantly related, its presence may be taken as showing the position of the true anterior border furrow. The important defining character of *Chelidonocephalus* is the presence of two anterior furrows. It is interesting to note that some forms comparable in this respect are to be found in the superfamily Rhyssometopacea Öpik (1967 : 272) described from the Mindyallan of Australia, for example *Rhyssometopus princeps* Öpik (1967 : pl. 27, fig. 1–3; text-fig. 96), if we can accept Öpik's 'frontal wrinkle' (*ibid.* : text-fig. 93) as homologous to our true border furrow. However, rhyssometopaceans show important differences from *Chelidonocephalus*, notably in having large palpebral lobes close to the glabella, and we are unable to classify our species with the Australian superfamily.

A comparative description of *Chelidonocephalus preannulatus* sp. nov. is given below, which extends the concept of the genus to include forms with larger palpebral lobes, closer to the glabella. They do not, however, approach rhyssometopaceans in this respect.

Chelidonocephalus preannulatus sp. nov.

Pl. 8, figs 6–8 ; Pl. 9, figs 1, 2, 5, 3 ?, 4 ?, 7 ?

DIAGNOSIS. *Chelidonocephalus* species with granulate surface sculpture. Anterior border broad and flat. Palpebral lobes larger, placed closer to the glabella than in *C. alifrons*, and convexity and furrow incision generally greater.

DERIVATION OF NAME. Latin – 'with a ring in front' – referring to the inflated, transverse preglabellar band.

HOLOTYPE. BM(NH) It 13503, incomplete cranidium partly preserving exoskeleton, figured on Pl. 9, fig. 2.

TYPE LOCALITY AND HORIZON. Mila Formation, Sanghabad, Taleghan Range, Alborz Mountains, northern Iran.

FIGURED MATERIAL. Cranidia It 13478 (Pl. 8, figs 6–8), It 13504 (Pl. 9, fig 5) ; free cheek It 13499 (Pl. 9, fig. 1) ; hypostoma, tentatively assigned, It 14020 (Pl. 9, figs 3, 4) ; pygidium, tentatively assigned, It 13460 (Pl. 9, fig. 7). Six unfigured fragments also present.

DISCUSSION. Since this species is similar to the type species *C. alifrons* in most proportional characters, a detailed description need not be repeated here. *C. preannulatus* differs from the type species in the following characters.

(i) Convexity (sag., exsag.) is greater, this being due to the increase in the downward deflexion of the fixed cheek in front of the palpebral lobes.

(ii) Anterior border is flat, not gently convex, forming a broad, horizontal rim around the cranidial margin. The border occupies about half (sag.) the preglabellar width, although the false border furrow, except on small cranidia, is ill defined.

(iii) Anterior branches of the facial sutures appear more divergent in dorsal view, this being due to the greater downward inclination of the preocular cheeks.

(iv) Length of palpebral lobes about half length of glabella. They are also closer to the glabella, such that the transverse width of the intraocular cheek at the anterior limit of the palpebral lobe is about half width of glabella at same section (0·7 times in *C. alifrons*).

(v) Furrows more deeply incised.

(vi) Surface sculpture of fine granules on glabella. Smooth areas on the glabella of one specimen (Pl. 8, figs 6–8) display the muscle insertion areas rather better than *C. alifrons*. Lateral occipital impression deep, producing a lateral narrowing of the occipital ring. 1P subcircular, indistinct, isolated within glabella near midline ; 2P of similar size and form adjacent to axial furrow opposite mid-part of palpebral lobe ; 3P opposite anterior end of palpebral lobe, narrow and transverse ; 4P of similar form, slightly anteriorly directed.

A free cheek (Pl. 9, fig. 1) shows a prominent eye socle, faint caeca radiate from the eye and there is a lateral continuation of the true and false border furrows which describe a ridge on the border. The counterpart shows the base of a strong genal spine.

A small hypostoma (Pl. 9, figs 3, 4) may belong to *C. preannulatus*. It is different from that assigned to *Koldiniella*, and from that of *Dorypyge*, so that

Chelidonocephalus is the most likely polymerid known from the present fauna to which it could belong. A distinctive feature is a prominent anterior hump on the middle body.

An incomplete associated pygidium is tentatively referred to this species because it shows traces of similar granular sculpture. The axis is wider than the flanks, tapers back, is rounded behind but tends to pass into a postaxial ridge ; it is composed of 4–5 rings and a terminal piece. Flanks show two distinct and one less clear pleural furrows. No interpleural furrows. There is a suggestion of a flattened lateral border.

REFERENCES

Annells, R. N., Arthurton, R. S., Bazley, R. A. B., & Davies, R. G. 1976. *Explanatory text of the Qazvin and Rasht Quadrangles Map.* Geological Quadrangles Nos E3 and E4. Geological Survey of Iran, Teheran.

Chang W.-T. 1957. Preliminary note on the Lower and Middle Cambrian stratigraphy of Poshan, Central Shantung. *Acta palaeont. sin.*, Peking, **5** : 29–31, 2 pls.

—— 1959. New trilobites from the Middle Cambrian of North China. *Acta palaeont. sin.*, Peking, **7** : 215–236, 4 pls.

—— 1963. A classification of the Lower and Middle Cambrian trilobites from North and Northeastern China, with description of new families and new genera. *Acta palaeont. sin.*, Peking, **11** : 475–487, 2 pls.

Daily, B. & Jago, J. B. 1975. The trilobite *Lejopyge* Hawle and Corda and the Middle – Upper Cambrian boundary. *Palaeontology*, London, **18** : 527–550, pls 62–63.

Dames, W. 1883. Cambrische Trilobiten von Laiu-Tung. *In* Richthofen, F. von, *China* **4** : 3–33, Pls 1, 2. Berlin.

Endo, R. & Resser, C. E. 1937. The Sinian and Cambrian formations and fossils of southern Manchoukuo. *Bull. Manchur. Sci. Mus.*, Mukden, **1**. ix + 474 pp., 73 pls.

Fortey, R. A. 1974. The Ordovician trilobites of Spitsbergen. I. Olenidae. *Skr. norsk Polarinst.*, Oslo, **160**. 81 pp., 24 pls.

Harrington, H. J. *et al.* 1959. Systematic descriptions, Class Trilobita. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Palaeontology*, **O**. xix + 560 pp., 415 figs. Lawrence, Kansas.

King, W. B. R. 1937. Cambrian trilobites from Iran (Persia). *Mem. geol. Surv. India Palaeont. Indica*, Calcutta, **22** (5). 22 pp., 2 pls.

—— 1955. *Iranoleesia*, new trilobite name. *Geol. Mag.*, Hertford, **92** : 86.

Kobayashi, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology, part 3. *J. Fac. Sci. Tokyo Univ.* sec. 2, **4** : 49–344, pls 1–24.

—— 1952. On *Mansuyia* and the Tsinanidae. *Trans. Proc. palaeont. Soc. Japan*, Tokyo, n.s. **5** : 145–154, pl. 13.

—— 1960. The Cambro-Ordovician formations and faunas of South Korea. Part VII, Palaeontology VI. *J. Fac. Sci. Tokyo Univ.* sec. 2, **12** : 329–420, pls 19–21.

—— 1966–67. The Cambro-Ordovician formations and faunas of South Korea. Part X, Stratigraphy of the Chosen Group in Korea and South Manchuria and its relation to the Cambro-Ordovician formations of other areas. Section B. The Chosen Group of North Korea and Northeast China. *J. Fac. Sci. Tokyo Univ.* sec. 2, **16** : 209–311. Section C. The Cambrian of Eastern Asia and other parts of the Continent. *Ibid.* : 381–535.

Kushan, B. 1973. Stratigraphie und Trilobitenfauna in der Mila-Formation (Mittelkambrium-Tremadoc) im Alborz-Gebirge (N-Iran). *Palaeontographica*, Stuttgart, A **144** (4–6) : 113–165, pls 26–34.

Lake, P. 1906–46. British Cambrian trilobites. *Palaeontogr. Soc.* (*Monogr.*), London. 350 pp., 47 pls.

Lazarenko, N. P. & Nikiforov, N. I. 1968. [Assemblages of trilobites from Upper Cambrian strata on the River Kulyumbe (northwestern Siberian Platform).] *Uchen. Zap. nauchno-issled. Inst. geol. arkt.*, Leningrad, Pal. Biostrat. **23** : 20–80, pls 1–15. [In Russian.]

Lermontova, E. V. 1951. [*Lower Cambrian trilobites and brachiopods from Eastern Siberia.*] 222 pp., 21 pls. Moscow (Vses. nauchno.-issled. geol. Inst. (VSEGEI)). [In Russian.]

Lochman, C. 1944. *In* Lochman, C. & Duncan, D. Early Upper Cambrian faunas of Central Montana. *Spec. Pap. geol. Soc. Am.*, Baltimore, **54**. 181 pp., 19 pls.

Longacre, S. A. 1970. Trilobites of the Upper Cambrian Ptychaspid Biomere, Wilberns Formation, Central Texas. *Rep. Invest. Bur. econ. Geol. Univ. Texas*, Austin, **66** : 1–70.

Lu Y.-H. 1954. Two new trilobite genera of the Kushan Formation. *Acta palaeont. sin.*, Peking, **3** : 425–438, 1 pl.

—— *et al.* 1965. [*Fossils of each group of China: Chinese Trilobites.*] 766 pp., 134 pls, 2 vols. Peking. [In Chinese.]

Öpik, A. A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Melbourne, **53**. 249 pp., 24 pls.

—— 1967. The Mindyallan fauna of north-western Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Canberra, **74**. (1) 404 pp. ; (2) 167 pp., 67 pls.

Palmer, A. R. & Gatehouse, C. G. 1972. Early and Middle Cambrian trilobites from Antarctica. *Prof. Pap. U.S. geol. Surv.*, Washington, **456-D**. 37 pp., 6 pls.

Rasetti, F. 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. *Smithson. misc. Collns*, Washington, **148** (3). 127 pp., 21 pls.

Reed, F. R. C. 1934. Cambrian and Ordovician fossils from Kashmir. *Mem. geol. Surv. India Palaeont. Indica*, Calcutta, **21** (2). 38 pp., 2 pls.

Resser, C. E. & Endo, R. 1937. *In* Endo, R., & Resser, C. E., q.v.

Rozova, A. V. 1960. [Upper Cambrian trilobites of the Salayr.] *Trudȳ Inst. Geol. Geofiz. sib. Otdel.*, Novosibirsk, **5**. 116 pp., 8 pls. [In Russian.]

—— 1964. [*Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the north-west Siberian Platform.*] 148 pp., 19 pls. Moscow, Akad. Nauk SSSR, Sibir. otdel. Inst. Geol. Geofiz. ('Nauka'). [In Russian.]

—— 1968. [Biostratigraphy and trilobites of the Upper Cambrian and Lower Ordovician of the north-west Siberian Platform.] *Trudȳ Inst. Geol. Geofiz. sib. Otdel.*, Moscow, **36**. 196 pp., 17 pls, 5 tab. [In Russian.]

Sivov, A. G. 1955. *In* Khalfina, L. L. [*Atlas of guide forms in the fossil faunas and floras of western Siberia.*] 327 pp. Moscow. [In Russian.] (*Fide* Kushan, not seen.)

Stöcklin, J. 1968. Structural history and tectonics of Iran : a review. *Bull. Am. Ass. Petrol. Geol.*, Tulsa, **52** : 1229–1258.

——, Ruttner, A. & Nabavi, M. 1964. New data on the Lower Paleozoic and Pre-Cambrian of North Iran. *Rep. geol. Surv. Iran*, Teheran, **1**. 29 pp., 1 pl.

Sun Y.-C. 1924. Contributions to the Cambrian faunas of North China. *Palaeont. sin.*, Peking, B **1** (4). 109 pp., 5 pls.

Taylor, K. & Rushton, A. W. A. 1972 [1971 on cover]. The pre-Westphalian geology of the Warwickshire Coalfield. . . . *Bull. geol. Surv. Gt Br.*, London, **35**. 152 pp., 12 pls.

Walcott, C. D. 1905. Cambrian faunas of China. *Proc. U.S. natn. Mus.*, Washington, **26** : 1–106.

—— 1913. The Cambrian faunas of China. *In* Willis, B. *et al.*, *Research in China* **3** : 1–276, pls 1–24. Carnegie Inst., Washington (publ. 54).

Westergård, A. H. 1946. Agnostidea of the Middle Cambrian of Sweden. *Sver. geol. Unders. Avh.*, Stockholm, C **477**. 140 pp., 16 pls.

—— 1948. Non-Agnostidean trilobites of the Middle Cambrian of Sweden. I. *Sver. geol. Unders. Avh.*, Stockholm, C **498**. 32 pp., 4 pls.

R. A. Fortey, Ph.D.
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

A. W. A. Rushton, B.A., Ph.D.
Institute of Geological Sciences
Exhibition Road
London SW7 2DE

Accepted for publication 9 February 1976

PLATE 8

Chelidonocephalus alifrons King 1937 (p. 336)

Mila Formation, Chal-i-Sheh, Loc. 3 of King 1937

FIG. 1. Plaster cast of lectotype (selected herein), incomplete cranidium, × 4. Specimen figured by King 1937 : pl. 2, fig. 8a, GSI 16311 (cast In 36893).

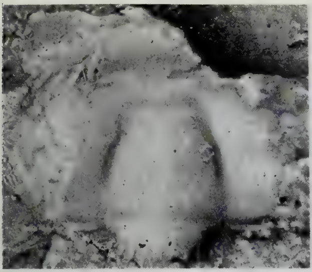
FIGS 2, 3, 5. Cranidium retaining cuticle, dorsal and lateral views × 5 ; Fig. 5, detail of right side of glabella showing surface sculpture of fine pitting, × 12·5. In 36895.

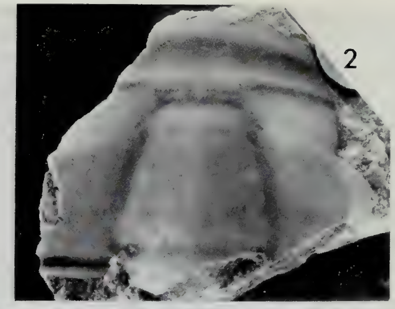
FIG. 4. Large exfoliated cranidium, showing caeca and form of facial suture, dorsal view, × 3. In 36896.

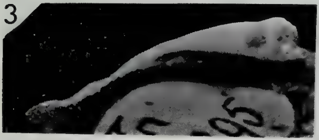
Chelidonocephalus preannulatus sp. nov. (p. 338 ; see also Pl. 9, figs 1–5, 7)

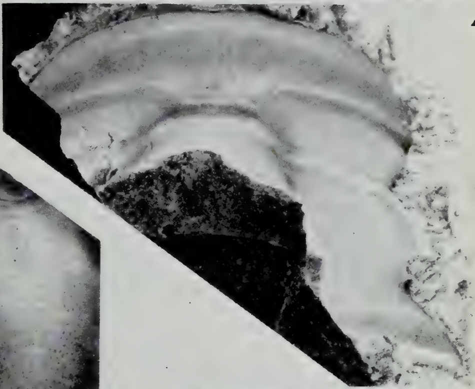
Mila Formation, near Sanghabad, Alborz Mountains

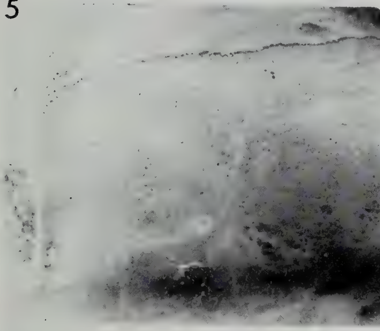
FIGS 6–8. Cranidium retaining cuticle, oblique lateral and dorsal views, × 4 ; Fig. 8, detail of right side of glabella to show sculptural difference from *C. alifrons*, × 12. It 13478.

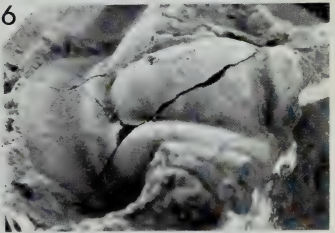

1

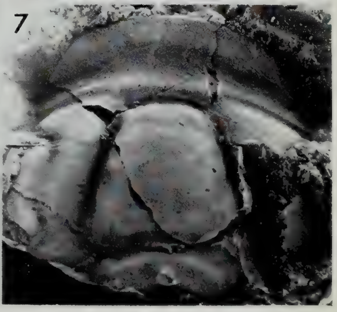

2


3


4


5


6


7

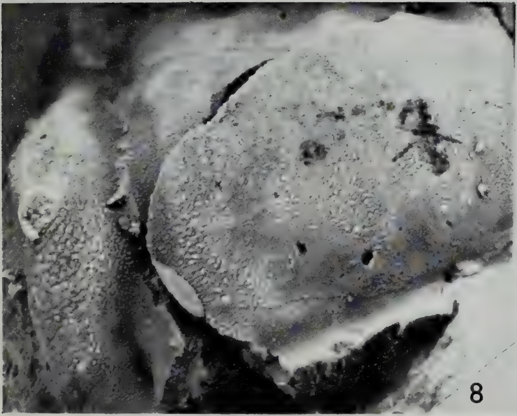

8

PLATE 9

Chelidonocephalus preannulatus sp. nov. (p. 338; see also Pl. 8, figs 6–8)

Mila Formation, near Sanghabad, Alborz Mountains

FIG. 1. Fragmentary free cheek, × 8. It 13499.

FIG. 2. Holotype, partially exfoliated cranidium, × 8. It 13503.

FIGS 3, 4. Hypostoma attributed to this species, ventral view, and lateral view to show anterior hump, × 10. It 14020.

FIG. 5. Smallest cranidium, × 15. It 13504.

FIG. 7. Pygidium probably attributable to this species, fragmentary, × 4. It 13460.

Iranoleesia pisiformis (King 1937) (p. 329)

Mila Formation, Ma'dan, Loc. 12 of King 1937

FIG. 6. Cast of holotype, incomplete cranidium, × 5. Original specimen figured by King 1937: pl. 2, fig. 6a, GSI 16305 (cast In 36890).

FIG. 8. Two cranidia, one retaining part of the cuticle and showing punctate surface sculpture, × 6. In 36910.

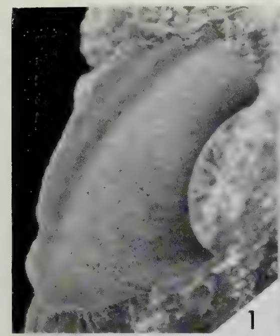
FIGS 9, 12. Internal mould of incomplete exfoliated cranidium, dorsal and lateral views, × 10. Note punctation on internal surface. In 36912.

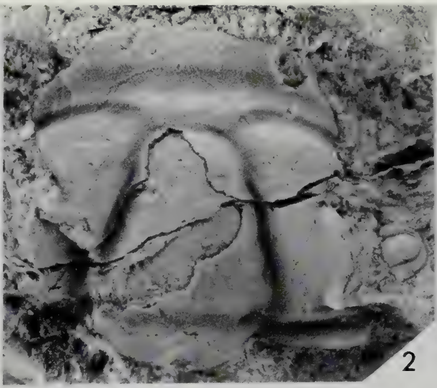
FIG. 10. Internal mould of cranidium, × 5. In 36911.

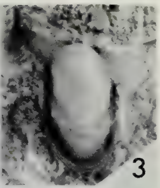
Anomocarella falconi (King 1937) ? (p. 331)

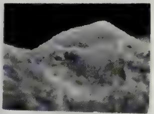
Mila Formation, Darreh Shu, Loc. 8 of King 1937

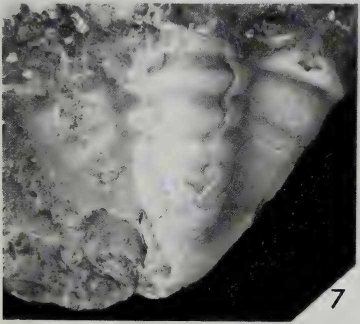
FIG. 11. Cast of incomplete pygidium, × 6; original figured by King 1937: pl. 2, fig. 7b, and there attributed to *A. falconi*, but possibly belonging to *Chelidonocephalus alifrons* (p. 332). GSI 16307 (cast In 36892).

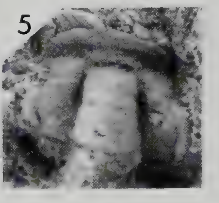

1

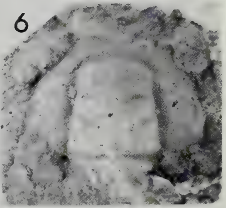

2

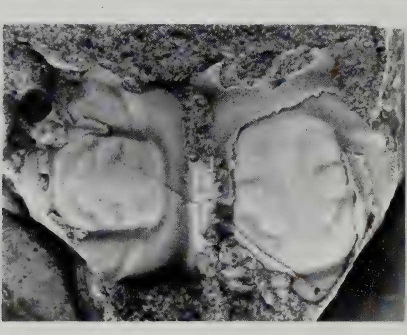

3

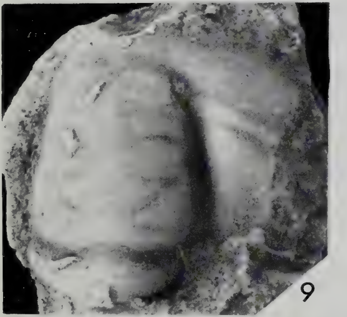

4

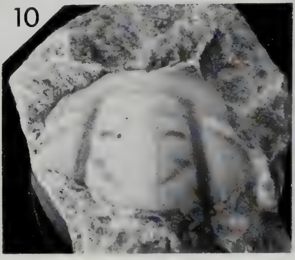

7

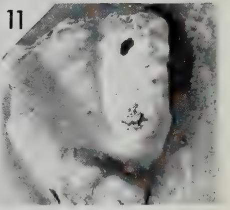

5


6


8


9


10


11

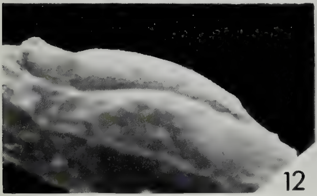

12

PLATE 10

Anomocarella falconi (King 1937) (p. 331; see also Pl. 9, fig 11)

Mila Formation, Darreh Shu, Loc. 8 of King 1937

FIG. 1. Latex impression taken from a cast of the holotype, external mould of cranidium, × 4. Original of King 1937: fig. 7a, GSI 16306 (cast In 36891).

FIG. 2. Small well-preserved cranidium retaining exoskeleton, dorsal view, × 10. In 36909a. Same rock fragment as cranidium, Fig. 4.

FIG. 3. Internal mould of large cranidium, × 5. In 36908.

FIGS 4, 5, 8. Cranidium with exoskeleton, incomplete over posterior part of glabella. Dorsal and oblique lateral views, × 10; Fig. 8, detail of right side to show fine granulation, × 20. In 36909b. Same rock fragment as cranidium, Fig. 2.

Koldiniella mitella Sivov 1955 (p. 333)

Mila Formation, near Sanghabad, Alborz Mountains

FIGS 6, 7. Well-preserved cranidium in palpebral and right lateral views, × 8. It 14021.

FIGS 9, 10. Pygidium, dorsal and posterior views, × 10, showing terrace lines confined to border. It 13477.

FIG. 15. Pygidium, relatively longer than previous specimen, × 10. It 14022.

FIG. 16. Hypostome tentatively assigned to this species, ventral view, × 10. It 13506.

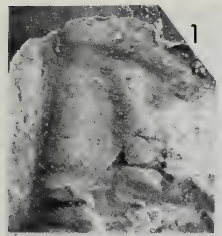
FIGS 13, 14. Small cranidium, possibly a small growth stage of *Koldiniella mitella* but may be referable to *Parakoldinia* (see text, p. 333), × 10. It 13476.

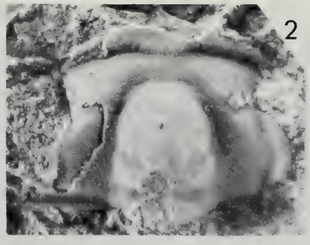
Tsinania ? sp. (p. 334)

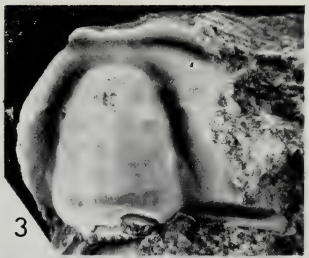
Mila Formation, near Sanghabad, Alborz Mountains

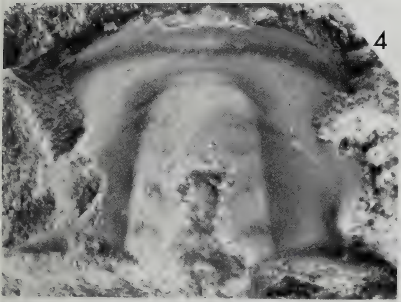
FIGS 11, 12. Incomplete cranidium, exfoliated, anterior and approximate palpebral views, × 10. It 13493.

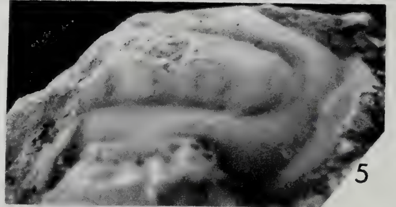
FIGS 17–19. Small cranidium, retaining exoskeleton, anterior and lateral views, × 7; Fig. 19, palpebral view, × 10. It 13458.

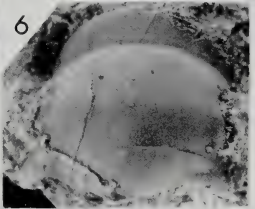

1

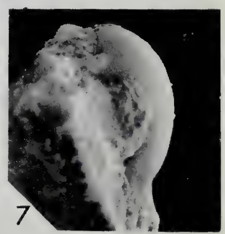

2

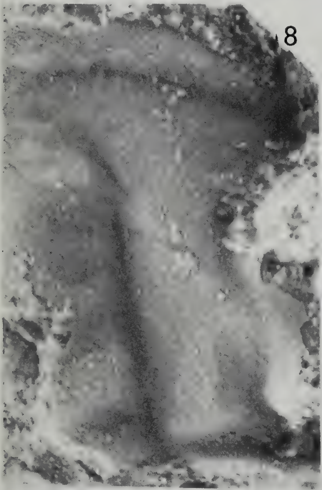

3

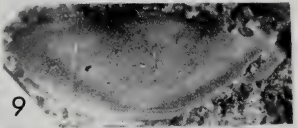

4

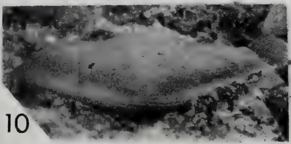

5

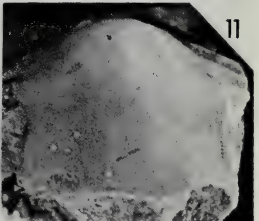

6

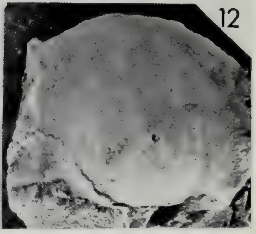

7

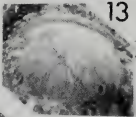

8

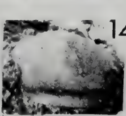

9

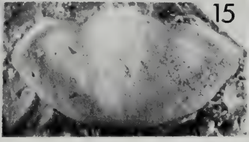

10

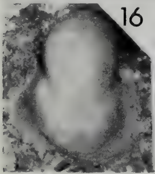

11

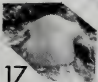

12

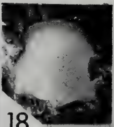

13


14


15


16


17


18

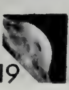

19

PLATE 11

Dorypyge sp. (p. 327)

Mila Formation, near Sanghabad, Alborz Mountains

FIGS 1, 2. Pygidium retaining most of exoskeleton, dorsal and oblique lateral views, × 6. Note impression of part of doublure posteriorly and thin subsidiary spine below third 'main' marginal spine on left. It 13461.

Hadragnostus edax sp. nov. (p. 324)

Mila Formation, near Sanghabad, Alborz Mountains

FIG. 3. Cephalon, glabella broken, × 10. It 13468.

FIGS 4–6. Pygidium, tectonically shortened, dorsal, posterior and left lateral views, × 10. Note terminal node (Fig. 5). It 13472.

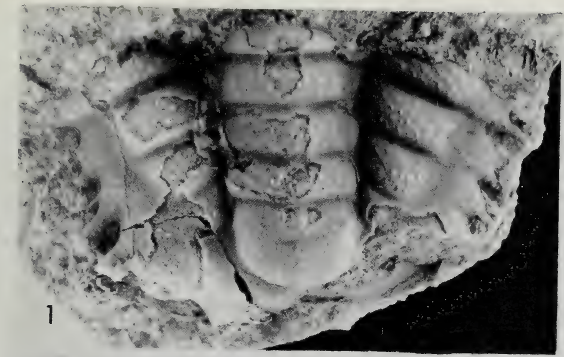
FIGS 7, 8, 12. Holotype pygidium, dorsal, posterior and left lateral views, × 10. Note articulating half-ring. It 13463.

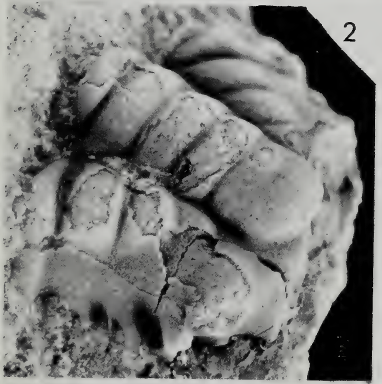
FIGS 9, 10. Cephalon cut by joints, dorsal and lateral views, × 10. It 13483a, on same block as Figs 14, 15.

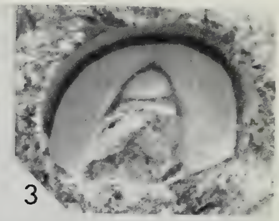
FIG. 11. Cephalon, showing rounded glabellar rear, × 10. It 14023.

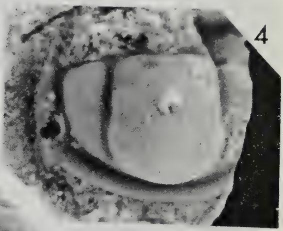
FIG. 13. Small pygidium, × 20. It 13471.

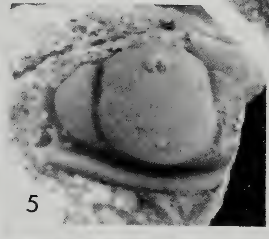
FIGS 14, 15. Cephalon, glabella damaged, dorsal and posterior views, × 15. Note faint node at posterior end of glabella. It 13483b, on same block as Figs 9, 10.

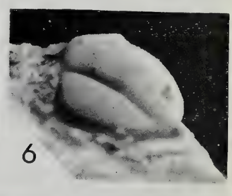

1

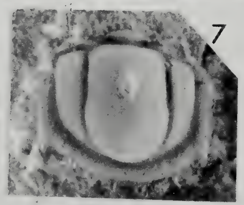

2

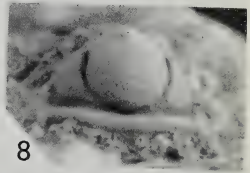

3

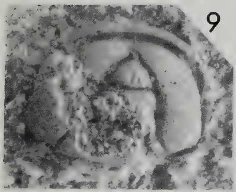

4

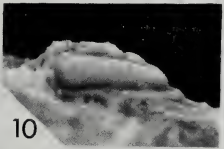

5

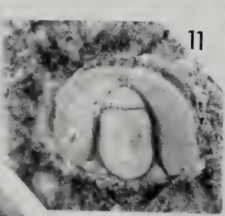

6

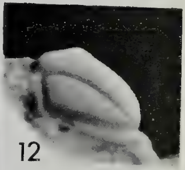

7

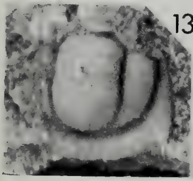

8

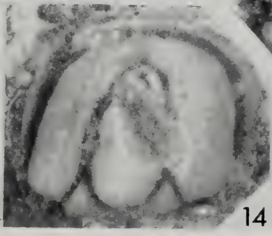

9


10


11


12


13


14

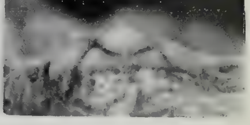

15

PLATE 12

Peronopsis fallax (Linnarsson 1869) aff. ***minor*** (Brögger 1878) (p. 326)

Mila Formation, near Sanghabad, Alborz Mountains

FIGS 1, 2. Large cephalon, latex cast of external mould, dorsal and lateral views, × 10. Note narrow axial furrow. It 13480b, on same block as Fig. 14.

FIGS 3, 4. Cephalon, slightly compressed laterally, exfoliated in region of axial furrow which appears wide, dorsal and lateral views, × 10. It 13480c.

FIGS 5. 8. Pygidium retaining exoskeleton, slightly deformed obliquely, dorsal and lateral views, × 10. It 13485.

FIG. 6. Large pygidium, partly exfoliated, × 10. It 13467.

FIG. 7. Pygidium, × 10. It 14025.

FIGS 9, 11. Cephalon, laterally compressed, exfoliated in region of axial furrow, lateral and dorsal views, × 10. Note elongate glabellar node and preglabellar depression. It 14024.

FIG. 10. Small cephalon exfoliated in region of axial furrow, × 10. Note preglabellar depression. It 14026.

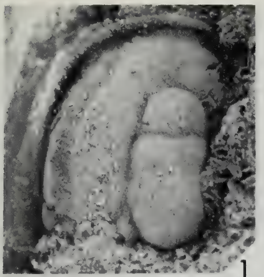
FIGS 12, 13. Pygidium, longitudinally compressed and partly exfoliated, dorsal and lateral views, × 10. It 13469.

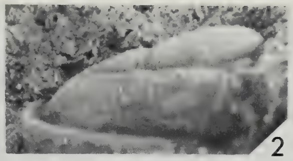
FIG. 14. Cephalon retaining exoskeleton, showing *Ptychagnostus*-like basal lobes, × 10. It 13480d, on same block as Figs 1, 2.

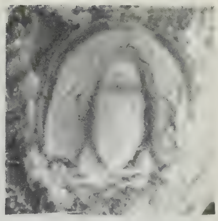
Peronopsis fallax (Linnarsson 1869) cf. ***minor*** (Brögger 1878) (p. 327)

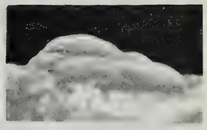
Mancetter Grits and Shales, Merevale No. 3. Borehole, near Nuneaton, Warwickshire, England

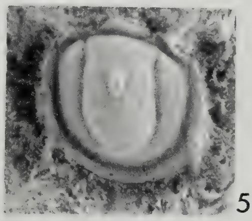
FIG. 15. Damaged internal mould, × 10. Institute of Geological Sciences, BDA 1781.

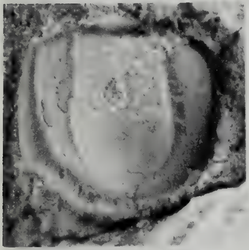

1

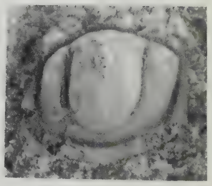

2

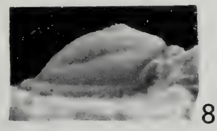

3

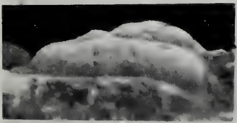

4

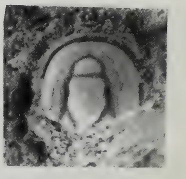

5

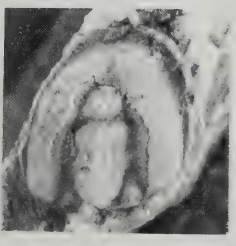

6

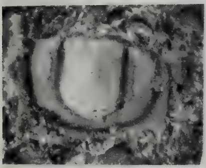

7

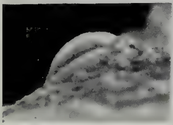

8

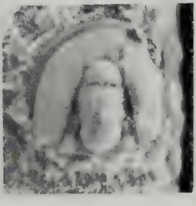

9

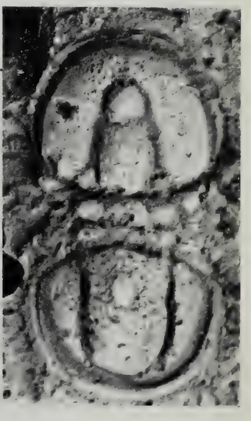

10


11


12


13


14


15

INDEX

to Vol. 27 No. 4 (Miscellanea)

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

Abhar 322
Acrospiriferinae 276
Acuminothyris 275, 282
Africa 309–12
Agnostidae, Agnostinae 322–5
Agnostoglossa simplexiformis 327
Agnostus pisiformis Zone 323, 327
  simplexiformis 327
Albian 301
Alborsella Zone 322
Alborz Mountains 321, 324, 338
algae 285
Alispirifer 275–6
Alokistocaridae 335
America 312, 319
Amesopleura 275
  novamexicana 278
Androstrobus 291
Anomocarella 322, 324, **330–1**, 332
  chinensis 330, 332
  concava 332
  falconi 321, 328, 330, **331–2**, 336; pl. 9, fig. 11; pl. 10, figs 1–5, 8
Anomocarellidae 331
Anomozamites 291
Ardennes–London landmass 285–6
Arizona 301
Asaphiscidae 324, 328–34
Auritamidae 335
Australia 311–2, 319, 337; see Mindyallan Stage
Avon 285

Baltagnostus 324
Bannister, Dr K. 298
Barbus 298
Baringo, Lake 295–6
Bath 285
Bathampton Down 285–6
Bathonian 285–6
Battus integer 326
Beast Cliff 291
Belgium 282
Bennettitaleans 291
Bisbee Quadrangle 301
Blastochaetetes bathonicus **285–6**, 287–8; pl. 2
Blountia 332
Bolland 278, 281–2
border furrows, true and false 337
brachiopods 275–84, 286, 301–4, 321
Brachyrhyncha 296–7
Brachythyrina 276, 282
Brunton, C. H. C. 275–84
bryozoa 285–6

California 301–4, 311
Cambrian 321–40
Carboniferous, Lower 275–84
Caspian Sea 321
Caytonia 291
Celsifornix 275
Chaetetida, Chaetetids 285–8
Chal-i-Sheh 322, 336
Chelidonocephalus 321–33, **334–6**, 337–40
  alifrons 321–3, 331–2, 335, **336–7**, 338; pl. 8, figs 1–5; pl. 9, fig. 11
  preannulatus 321, 332–3, 336–7, **338–9**; pl. 8, figs 6–8; pl. 9, figs 1–5, 7
  sp. 322–3
Chile 319
Cirencester 285–6
Clitheroe 278
Cnidaria 285
Conocoryphidae 324
coprolites 289–94, 290*; pl. 3, fig. 4
coral 286
Cotswolds 285–6
crabs, freshwater 295–300
Cracow 303
Crepicephalus Zone 323
Cretaceous 301–4
Croiset collection 308
Cyclothyridinae 302–3
Cyclothyris 301–4
  americana 301
  antidichotoma 303; pl. 5, figs 2–3
  densleonis 301, 302*, **302–3**; pl. 5, figs 1, 4
  latissima 303
  mirabilis 303
  subtrigonalis 301
Cyrtia 276
Czekanowskia 291

Darreh Shu 322, 331
Davidson collection 277–8
Davies, Dr R. G. 321–2

Deltaic, Lower 289
Delthyrididina 276
Devonian, Upper 282
Dictyella 324
Dictyites 324
Dorypyge 322–3, **327**, 333, 338 ; Zone 322–3
  aenigma 333
  iranensis 328
  khademi khademi 328
    papillosa 328
  richthofeni 327
    laevis 328
    laiwuensis 328
    n. subsp. aff. *richthofeni* 327
  sp. 321, 323, **327–8** ; pl. 11, figs 1–2
Dorypygidae 327–8
Dovedale 277, 279–80
Drepanura Zone 322–3
  (*Spinopanura*) 322
Dublin 282

echinoderms 286
Eleutherokomma 275–6
Elliott, G. F. 285–8
England 301, 303
eretes Zone 323
Europe 301
Eymekops rectangularis 335

Faringdon 303
Fermanagh 278–81
fish 291, 298
flamingos 305–14
Florida 311
Forest Marble 286
Fortey, R. A. 321–40
France 285, 303, 305, 307, 309
Fusella 275, **276–8**, 279–84
  convoluta 281–2
  fusiformis 275–7, **278–82** ; pl. 1, figs 5–12, 20–21
  llanoensis 278
  rhomboidea 275, 277–8, 280*, 281*, 281–2 ; pl. 1, figs 13–19
  roemerianus 282
  tornacensis 277
  triangularis 282
  trigonalis 281–2

Germany 309
Gervaisia 307–8, **308–9**
  croiseti 305, 306*, 307*, 308, 310
Gilbertson collection 278, 282
Gloucestershire 285
Grandioculus falconi 330
  megalurus 330
Gristhorpe Bed 291

Haanakdar 322
Hadragnostus **324**
  edax 321, 323, **324–5** ; pl. 11, figs 3–15
  las 323–5
  modestus 323–5
Harrison, C. J. O. 305–20
Hartshillia 324
herbivores 289
Hill, C. R. 289–94
Hinde collection 285
Holloway, Miss M. L. 312, 319
Horsetown Group 301
Hundwarella 328
Hydrozoa 285
Hypermecaspis 328

Illaenidae 333
Illaenuridae 333
Illaenurus 333
  caneus 334
Iniotoma 328
Inouyella 335
  peiensis 335
insects 291
Iran 321–40, 322*
Irania 328
  falconi 328, 330–1
  pisiformis 328–9
Iranoleesia 322, 324, **328–9**, 330 ; Zone 322
  falconi 321, 328, 330
  pisiformis 321–2, 328, **329–30** ; pl. 9, figs 6, 8–10, 12

Jell, Dr P.
Jurassic 285–94

Kabarsero 295
Kalimale 295–6
Kamwina 295–6, 298
Kaolishania Zone 322
Kashmir 328
Keates, C. 319
Kenya 295–300, 305, 309, 311
Kingstonia 333
Koldinia 324
Koldiniella 322–3, **332–3**, 338
  convexa 333
  mitella 321–3, 329, 332, **333–4** ; pl. 10, figs 6–7, 9–10, 13–16
  prolixa 333

Kootenia 328
Kulyumbe 323

laevigata Zone 323
Leakey, Dr L. S. B. 311, 317
Leighton Buzzard 303
Leistegiidae 335
Lejopyge laevigata Zone 323
Licharewiinae 276
Limekiln Pit 285
Liopeishania 333
  lubrica 333
  spannensis 333
Lirrangopotamonautes see *Potamonautes*
Llanoaspis walcotti 335

Macelloura 333
Ma'dan 322, 329
mammal 291–2
Mapan Formation 332
Mapania 331
Mapaniidae 335
Maryvillia 332
Meneviella 324
Mexico 301, 312
Mila Formation 321, 323–4, 331, 338
  zones 322
Mila Kuh 322
Mindyallan Stage 323, 328, 337
Miocene 295–300, 305–14, 319
Mirifusella 277
molluscs 286
Montana 323
Morris, S. F. 295–300, 321
Mucrospiriferidae 275–82
Mural Limestone 301

Nailsworth 285
Nairobi 296
Namanoia 335
Namanoiidae 335
New Mexico 278
New South Wales 278
Ngorora Formation 295–300
Nilssoniopteris vittata 291
Nuneaton 323

Olduvai 315–20
Oligocene 305–14
oncolites 285
Ordosia 335
  fimbricauda 335
ornithopod dinosaur 291
Orthopotamonautes see *Potamonautes*

ostracods 295
Owen, E. F. 301–4

Paeckelmanella 276, 282
Paeckelmanellidae 276
Papyriaspididae 335
Parakoldinia 333; pl. 10, figs 13–14
  plana 334
  ? sp. 321
Paris Basin 285
Pedinocephalina – Toxotis (?) Zone 323
Peichishania 335
  rectangularis 335
Peishania 333
  lubrica 333
Pelecani 315
Pelecanidae 315
Pelecaniformes 315
Pelecanus 315–19
  aethiopicus **315–19**, 316*; pl. 7
  conspicillatus 318–19
  crispus 316*, 318–19
  erythrorhynchus 318–19
  gracilis 319
  grandiceps 319
  halieus 319
  intermedius 319
  occidentalis 318–19
    thagus 319
  odessanus 319
  onocrotalus 316*, 318–19
  proavus 319
  rufescens 316*, 318
pelican 315–20
Pérignat 308
Permian 282
Peronopsis 324, **326**
  fallax ferox 326
    aff. *minor* 321, 323, **326–7**; pl. 12, figs 1–14
    cf. *minor* 323, 326; pl. 12, fig. 15
  integer 326
Peru 319
Phoeniconaias 305, 308–11
  floridanus 311–12
  gracilis 311
  minor 305, 306*, 307*, 309, 309*, 311
  novaehollandiae 311
  stocki 312
Phoeniconotius eyrensis 312
Phoenicoparrus 305, 308, 310
  andinus 305
  jamesi 305, 306*, 307*, 309*
Phoenicopteridae 310

Phoenicopterus 305, 308, 310
  aethiopicus 305, 309*, 310*, **311–12**; pl. 6
  copei 312
  croiseti 305, **307–8**
  minutus 311
  ruber 305, 307*, 308–11
    antiquorum 305
    chilensis 305, 306*, 307*, 309*, 310*
    ruber 305
Pickford, Dr M. 295
plant cuticles 289–92
Pleistocene 311–2, 315–20
Plethometopus convergens 334
  obtusus 334
Plethopeltoides lepidus 334
Pliocene 311–2, 319
Poshania 335
  poshanensis 335
Poshauia 335
Potamidae 296–7
Potamon (*Potamonautes*) *lirrangensis* 296
Potamonautes **296**, 297–8
  lirrangensis 296
  perlata 296
  (*Lirrangopotamonautes*) 295, **296**, 297
    lirrangensis 296, 298
    tugenensis 295, **296–7**, 298; pl. 4
  (*Orthopotamonautes*) 295, 297
    depressus 298
    johnstoni 298
Prochuangia Zone 322
Protohedinia 329
Pterophyllum 291
Pterospirifer 275–6, 282
Ptilophyllum 289–94
  pectinoides 290*, 291; pl. 3
Ptychagnostus 327
  atavus 326
ptychoparioids 321, 323
Puy-de-Dôme 307
pygostyle 297

Qanli-Chapoghlu 322
Qazvin 321
Quadragnostidae 326–7
quasivespa Zone 323
Queensland 323

rabbits 289, 291
reptiles 291
Rhynchonella 301
  densleonis 301–2
Rhynchonellidae 301–3
Rhyssometopacea 335–7
Rhyssometopus princeps 337
Rift Valley 298
Rissoné, A. 275–84
Roseberry Topping plant bed 289–92
Rushton, A. W. A. 321–40
Rusinga Island 305, 309, 311

Salair 323
Sanghabad 321–2, 324, 338
Saukia Zone 322
Scandinavia 323
Schulze-Ammonia maceration 291
Sclerospongiae 286
Shahmirzad 322
Shasta County 301
sheep 291–2
Shiraz 321
Siberia 323
Solenites 291
Spinopanura see *Drepanura*
Spirifer 276
  bicarinata 276, 282
  convoluta 282
  cuspidatus 281–2
  distans 282; pl. 1, figs 1–4
  fusiformis 276, 278
  mundula 278
  novamexicana 278
  rhomboidea 277
  rhomboides 276
  roemerianus 282
  tornacensis 277
  triangularis 282
Spiriferacea 275–82
Spiriferidae 275–6
Spiriferidina 276
Spirifinaella 276
sponges 286
stromatoporoids 285
Strophopleura 275, 282
  anterosa 278
Strophopleurinae **275–6**, 277–82
Syringothyridacea 276
Syringothyrididae 277
Syringothyris 281–2
  cuspidatus 281–2

tabulates 285
Taitzuia 335
  insueta 335
Taleghan Range 324, 338
Tang-i-Tehbud Bezuft 322
Tanout 298

Tanzania 315, 317
Tehran 321
Tengfengiidae 329
Tennessee 335
Terebratulidae 301
Thelphusa perlata 296
Thomas, Dr H. H. 289
Tiltup's End 285-6
Tomes collection 285
Tournaisian 282
Toxotis see *Pedinocephalina*
Treak Cliff 281-2
trilobites 321-40
  effaced 324, 332-3
Tsinania 324, **334**
  caneus 334
  ? sp. 321, 323, **334**; pl. 10, figs 11-12, 17-19
Tsinaniidae 324, 333
Tugen Hills 295-6

Unispirifer 277-8

Victoria, Lake 309, 311
Viséan 279-82
Voiseyella 275-6, 278, 282
  anterosa 278
  novamexicana 278

WALKER, C. A. 305-20
Wanwanoglobus convexus 334
Williamsonia 292
  hildae 291
  leckenbyi 291
Witchell collection 285

Xanthoidea 296-7

Yorkshire 289-94

Zagros Thrust 321

A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. COX, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. OUT OF PRINT.
2. EL-NAGGAR, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £11.
3. DAVEY, R. J., DOWNIE, C., SARJEANT, W. A. S. & WILLIAMS, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £8.20.
3. APPENDIX. DAVEY, R. J., DOWNIE, C., SARJEANT, W. A. S. & WILLIAMS, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.
4. ELLIOTT, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 16 Text-figures. 1968. OUT OF PRINT.
5. RHODES, F. H. T., AUSTIN, R. L. & DRUCE, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 313; 31 Plates; 92 Text-figures. 1969. £13.10.
6. CHILDS, A. Upper Jurassic Rhynchonellid Brachiopods from Northwestern Europe. Pp. 119; 12 Plates; 40 Text-figures. 1969. £5.25.
7. GOODY, P. C. The relationships of certain Upper Cretaceous Teleosts with special reference to the Myctophoids. Pp. 255; 102 Text-figures. 1969. £7.70.
8. OWEN, H. G. Middle Albian Stratigraphy in the Anglo-Paris Basin. Pp. 164; 3 Plates; 52 Text-figures. 1971. £7.20.
9. SIDDIQUI, Q. A. Early Tertiary Ostracoda of the family Trachyleberididae from West Pakistan. Pp. 98; 42 Plates; 7 Text-figures. 1971. £9.60.
10. FOREY, P. L. A revision of the elopiform fishes, fossil and Recent. Pp. 222; 92 Text-figures. 1973. £11.35.
11. WILLIAMS, A. Ordovician Brachiopoda from the Shelve District, Shropshire. Pp. 163; 28 Plates; 11 Text-figures; 110 Tables. 1974. £12.80.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA

THE AMMONITE FAMILY PHYLLOCERATIDAE

W. J. KENNEDY
AND
H. C. KLINGER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27 No. 5
LONDON: 1977

BRITISH MUSEUM
GENERAL
1977
LIBRARY
NATURAL HISTORY

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA

THE AMMONITE FAMILY PHYLLOCERATIDAE

BY
WILLIAM JAMES KENNEDY
University of Oxford
AND
HERBERT CHRISTIAN KLINGER
South African Museum, Cape Town

Pp. 347–380 ; 15 *Plates* ; 9 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 27, No. 5
LONDON: 1977

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 27, *No.* 5 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

© Trustees of the British Museum (Natural History), 1977

BRITISH MUSEUM (NATURAL HISTORY)

Issued 27 January 1977 *Price* £6·10

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA

THE AMMONITE FAMILY PHYLLOCERATIDAE

By W. J. KENNEDY & H. C. KLINGER

CONTENTS

		Page
	Abstract	349
I.	Introduction	350
	Location of Specimens	350
	Field Localities	351
	Dimensions of Specimens	351
II.	Systematic palaeontology	351
	Genus *Phylloceras*	351
	Subgenus *Phylloceras*	352
	Phylloceras (*Phylloceras*) *serum*	352
	Subgenus *Hypophylloceras*	354
	Group of *Phylloceras* (*Hypophylloceras*) *thetys*	354
	Phylloceras (*Hypophylloceras*) *subalpinum ellipticum*	355
	Phylloceras (*Hypophylloceras*) *aphrodite*	358
	Group of *Phylloceras* (*Hypophylloceras*) *velledae*	359
	Phylloceras (*Hypophylloceras*) *velledae*	360
	Phylloceras (*Hypophylloceras*) *velledae velledae*	360
	Phylloceras (*Hypophylloceras*) *velledae inflatum*	362
	Phylloceras (*Hypophylloceras*) sp. aff. *velledae*	363
	Group of *Phylloceras* (*Hypophylloceras*) *seresitense*	363
	Phylloceras (*Hypophylloceras*) *seresitense*	363
	Phylloceras (*Hypophylloceras*) *seresitense seresitense*	364
	Phylloceras (*Hypophylloceras*) *androiavense*	365
	Phylloceras (*Hypophylloceras*) *woodsi woodsi*	366
	Phylloceras (*Hypophylloceras*) *mikobokense*	368
	Genus *Partschiceras*	369
	Partschiceras umzambiense	370
	Parschiceras sp. juv. ? cf. *baborense*	371
	Genus *Carinophylloceras*	372
	Carinophylloceras collignoni	373
III.	Acknowledgements	374
IV.	References	374
V.	Index	378
VI.	Erratum	380

ABSTRACT

Phylloceratid ammonites are present in rocks of Barremian, Albian, Cenomanian, Santonian, Campanian and Maastrichtian ages in Zululand and Natal, South Africa. They form a substantial proportion of the normally coiled ammonite fauna during the Barremian and Albian, but are rare in Aptian and post-Albian faunas. The following forms are described below.

Phylloceras (*Phylloceras*) *serum* (Oppel), *P.* (*Hypophylloceras*) *subalpinum* (d'Orbigny) *ellipticum* Kossmat, *P.* (*Hypophylloceras*) *aphrodite* Fallot & Termier, *P.* (*Hypophylloceras*) *velledae velledae* (Michelin), *P.* (*Hypophylloceras*) *velledae* (Michelin) *inflatum* Collignon, *P.* (*Hypophylloceras*) sp. aff. *velledae* (Michelin), *P.* (*Hypophylloceras*) *seresitense seresitense* Pervinquière, *P.* (*Hypophylloceras*) *androiavense* Besairie, *P.* (*Hypophylloceras*) *woodsi woodsi* van Hoepen, *P.* (*Hypophylloceras*) *mikobokense* Collignon, *Partschiceras umzambiense* (van Hoepen), *Partschiceras* sp. juv. cf. *baborense* (Coquand) and *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy.

Eight of these species are new records from the area.

I. INTRODUCTION

THE Phylloceratidae are the root stock of the Jurassic and Cretaceous phylloceratids, appearing in the Lower Jurassic (Sinemurian) and ranging to the Upper Cretaceous (Lower Maastrichtian). They have a world-wide distribution, but for most of the Cretaceous they are typically rare in the boreal region of north-western Europe and in the western interior of North America. In South Africa, species are known from the Barremian to Lower Maastrichtian, and are relatively common in the Barremian and Albian.

The following species are described below :

Phylloceras (*Phylloceras*) *serum* (Oppel)
P. (*Hypophylloceras*) *subalpinum* (d'Orbigny) *ellipticum* Kossmat
P. (*Hypophylloceras*) *aphrodite* Fallot & Termier
P. (*Hypophylloceras*) *velledae velledae* (Michelin)
P. (*Hypophylloceras*) *velledae* (Michelin) *inflatum* Collignon
P. (*Hypophylloceras*) sp. aff. *velledae* (Michelin)
P. (*Hypophylloceras*) *seresitense seresitense* Pervinquière
P. (*Hypophylloceras*) *androiavense* Besairie
P. (*Hypophylloceras*) *woodsi woodsi* van Hoepen
P. (*Hypophylloceras*) *mikobokense* Collignon
Partschiceras umzambiense (van Hoepen)
Partschiceras sp. juv. cf. *baborense* (Coquand)
Carinophylloceras collignoni Klinger, Wiedmann & Kennedy

Location of Specimens

The following abbreviations are used to indicate the repositories of the material studied :

BM(NH)	British Museum (Natural History), London
EMP	École des Mines, Paris
MHNP	Muséum d'Histoire Naturelle, Paris
SAM	South African Museum, Cape Town
SAS	South African Geological Survey, Pretoria
TM	Transvaal Museum, Pretoria
UPE	University of Pretoria, Pretoria

Field Localities

Outline details of field localities referred to in this paper are given by Kennedy & Klinger (1975); full descriptions of sections are deposited in the Palaeontology Library of the British Museum (Natural History).

Dimensions of Specimens

All dimensions given below are in millimetres:

D = Diameter
Wb = Whorl breadth
Wh = Whorl height
U = Umbilicus

Figures in parentheses are dimensions as a percentage of the total diameter.

II. SYSTEMATIC PALAEONTOLOGY

Class *CEPHALOPODA* Cuvier 1797

Subclass *AMMONOIDEA* Zittel 1884

Order PHYLLOCERATIDA Arkell 1950

Superfamily **PHYLLOCERATACEAE** Zittel 1884

Family **PHYLLOCERATIDAE** Zittel 1884

Subfamily **PHYLLOCERATINAE** Zittel 1884

Genus ***PHYLLOCERAS*** Suess 1865

Type species. *Ammonites heterophyllus* J. Sowerby 1820.

Discussion. An extensive and useful review of the scope and interpretation of *Phylloceras* and its subgenera has been given by Wiedmann in a series of publications (1962a, b, 1964; Wiedmann & Dieni 1968). He stresses the slight differences of both species and genera within the phylloceratids, and regards many of the taxa proposed by previous workers as of little value on either phylogenetic or stratigraphic grounds. With minor reservations, his conclusions are accepted here, and they clarify the relations between the bewildering host of taxa referred to the group. Our following discussions thus rest heavily on his work, but are included here as a review of work otherwise available only in German.

The genus *Phylloceras* is thus typified by the group of *Phylloceras heterophyllum*. *Rhacoceras* Hyatt 1867 and *Heterophylloceras* Kovacs 1939 are both objective synonyms, while the poorly defined *Xeniophylloceras* Buckman 1921, *Hantkeniceras* Kovacs 1939 and *Pseudophylloceras* Beznosov 1958 do not bear separation on either gross morphological features or sutural details. Furthermore, fasciculate ribbing occurs in some *Phylloceras* s.s., suggesting that the Pseudophylloceratinae (Beznosov 1958) – genera such as *Neophylloceras* Shimizu 1934 and *Epiphylloceras* Collignon 1956 – do not bear separation from *Phylloceras* s.s. The following subgenera can be recognized.

Phylloceras Suess 1865, type species *Ammonites heterophyllus* J. Sowerby 1820, Lower Jurassic to Lower Cretaceous.

Zetoceras Kovacs 1939, type species *Ammonites zetes* d'Orbigny 1850, Lower to Middle and ? Upper Jurassic.

Geyeroceras Hyatt 1900, type species *Ammonites cylindricus* J. de C. Sowerby 1831, Lower Jurassic.

Hypophylloceras Salfeld 1924, type species *Phylloceras onoense* Stanton 1895, Cretaceous.

Subgenus ***PHYLLOCERAS*** Suess 1865

Phylloceras (Phylloceras) serum (Oppel)

(Fig. 1 ; Pls 1–2 ; Pl. 3, figs 1–2)

1865 *Ammonites serus* Oppel : 550.
1868 *Phylloceras serum* Oppel ; Zittel : 66, pl. 7, figs 5, 6.
1885 *Phylloceras semistriatum* d'Orbigny ; Neumayr : 83, pl. 1, fig. 2 (non d'Orbigny).
1890 *Phylloceras serum* Oppel ; Toucas : 574, pl. 13, fig. 2.
? 1891 *Phylloceras* cf. *thetys* d'Orbigny ; Sayn : 141, pl. 1, fig. 1.
1901 *Phylloceras serum* Oppel var. *perlobata* Sayn : 7, text-fig. 3, pl. 1, figs 6–8.
1901 *Phylloceras thetys* d'Orbigny ; Sayn : 36, pl. 1, fig. 3 only.
1907 *Phylloceras serum* Oppel ; Pervinquière : 12, pl. 1, fig. 3.
1914 *Phylloceras serum* Oppel var. *perlobata* Sayn ; Zwierzycki : 33, pl. 4, figs 2, 3.
1949a *Phylloceras spathi* Collignon : 63, pl. 9, figs 1–1b.
? 1949a *Phylloceras robionense* Collignon : 64, 65, text-figs 1–1a.
1951 *Phylloceras serum* (Oppel) ; Arnould-Saget : 5, pl. 1, fig. 5.
1957 *Hyporbulites betieri* Busnardo ; Busnardo & David : 84, pl. 1, figs 1–2 ; text-figs 4, 5.
1960 *Euphylloceras serum* Oppel ; Drushchitza & Kudryavtseva : 251, pl. 1, fig. 8.
1960 *Phylloceras serum* Oppel ; Collignon : pl. 134, figs 506, ? 507.
1962a *Phylloceras serum* Oppel ; Collignon : 20, pl. 181, fig. 817 ; 33, pl. 186, fig. 853 ; 76, pl. 214, fig. 916.
? 1962a *Phylloceras spathi* Collignon ; Collignon : 74, pl. 203, fig. 915 ; pl. 204, fig. 915a.
1966 *Phylloceras* cf. *perlobatum* Sayn ; Rawson : 455, pl. 72, figs 1–3.
? 1968 *Ph.* (*Phylloceras*) *spathi* Collignon ; Wiedmann & Dieni : 22.
1968 *Ph.* (*Phylloceras*) *serum* (Oppel) ; Wiedmann & Dieni : 20.

LECTOTYPE. The specimen figured by von Zittel (1868) as his pl. 7, fig. 5 is herein designated lectotype.

MATERIAL. Fourteen specimens, all from the Upper Barremian (Barremian I), Loc. 170, Mlambongwenya Spruit, northern Zululand. BM(NH) C78652-61. SAS LJE 132b, 54/19, 54/33, Z19.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Zittel 1868 : 66	106·0	(28)	(60)	0·46	
Collignon 1960 : pl. 134, fig. 566	96·0	35 (36)	57 (59)	0·61	
Collignon 1962a : pl. 204, fig. 916	123·0	43·0 (35)	72·0 (59)	0·60	
BM(NH) C78657	86·4	28·2 (33)	49·4 (57)	0·57	6·4 (7)
BM(NH) C78660	120·5	44·5 (37)	70·8 (59)	0·62	8·6 (7)

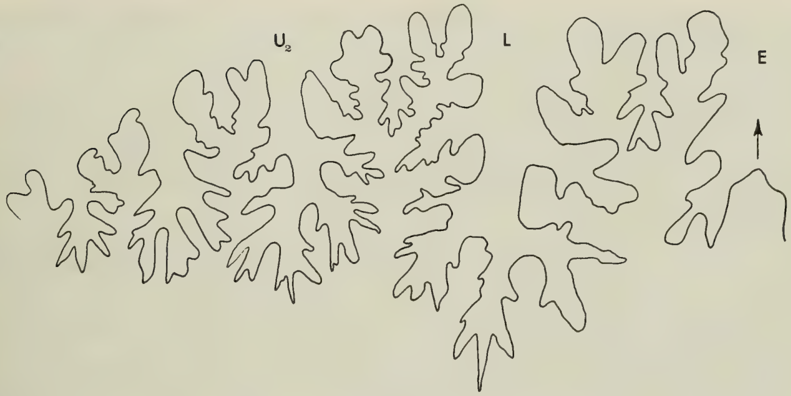


FIG. 1. External suture line of *Phylloceras* (*Phylloceras*) *serum* Oppel. SAS LJE 132b, ×6.

Phylloceras spathi, from Collignon 1949a : 62.					
Example 1	112·0	46·0 (41)	63·0 (56)	0·73	6·0 (5)
Example 2	110·0	44·0 (40)	65·0 (59)	0·67	6·0 (5)
Example 3	113·0	40·0 (35)	66·0 (53)	0·60	6·0 (5)
Phylloceras robionense, from Collignon 1949a : 64.					
Holotype	141·0	45·0 (32)	81·0 (57)	0·55	5·0 (4)

DESCRIPTION. The coiling is very involute with a tiny, deep umbilicus measuring 7% of the diameter. The umbilicus is undercut, the umbilical wall rounded, and the umbilical shoulder gently sloped, so that there is a shallow conical depression surrounding a deep umbilical pit. The whorl section is a compressed oval, with flattened subparallel lower flanks and upper flanks which converge towards broadly rounded shoulders and a broad, rounded venter.

The shell surface is ornamented by fine, dense, flexuous striae. These arise at the umbilical seam and are very fine, dense and crowded over the umbilical wall, shoulder and lower flank, strengthening on the outer flank and venter. They pass straight across the lower flank, flex slightly backwards some way below mid-flank, to sweep gently forwards over the upper flank and shoulder. They pass across the broad venter with a faint forwards projection. Internal moulds bear a fainter but comparable ornament.

The suture line is complex, phylloid, the saddles having tetraphylloid terminations, as shown in Fig. 1.

DISCUSSION. Flattened sides, broad venter, flexuous ornament and tetraphylloid saddles clearly place our specimens within the range of variation ascribed to *Phylloceras* (*Phylloceras*) *serum* by Collignon (1962), Arnould-Saget (1951) and Wiedmann & Dieni (1968), whom we follow in regarding Sayn's variety *perlobata* and the '*Hyporbulites*' *betieri* of Busnardo as synonyms. *Phylloceras* (*Phylloceras*) *spathi* Collignon is very close to *P.* (*P.*) *serum* in ornament, and overlaps in relative proportions, the large specimen figured by Collignon (1962a : pl. 203, fig. 915) having a similar suture, which suggests that this species may also fall into synonymy. Wiedmann & Dieni (1968 : 22), however, state that *P.* (*P.*) *spathi* lacks ornament on internal moulds and differs from *P.* (*P.*) *serum* mainly in whorl shape. *Phylloceras robionense*, from the Barremian of southern France (Basses-Alpes), may also be a synonym.

P. (*P.*) *serum* has, on occasion, been confused with *Phylloceras* of the *thetys* group, with which it is homoeomorphic ; these forms have, however, diphylloid saddle terminations as do forms such as *Phylloceras sablyense* Karakash.

Occurrence. *Phylloceras* (*Phylloceras*) *serum* has a long time range and a wide geographic distribution, which may be summarized as follows :
Upper Jurassic (Tithonian) of central Europe (Stramberg Limestone), southern France, north Africa (Tunisia) and Madagascar ; Lower Cretaceous of southern France (Valanginian and ? Barremian), Sardinia (Valanginian), Madagascar (Hauterivian and Valanginian) and Zululand (Barremian).

Subgenus ***HYPOPHYLLOCERAS*** Salfeld 1924

Type species. *Phylloceras onoense* Stanton 1895.

Diagnosis. Compressed, discoidal involute phylloceratids, inner whorls occasionally constricted ('*Aphroditiceras*', '*Euphylloceras*', '*Goretophylloceras*'). Ornament of both shell and moulds consists of weak radial striae, strengthening on the venter ; occasionally fasciculate in the umbilical region ('*Neophylloceras*', '*Epiphylloceras*'). Suture with diphylloid ('*Goretophylloceras*'), tetraphylloid ('*Hyporbulites*') or polyphylloid saddles (from Wiedmann 1964 : 173).

Discussion. Following Wiedmann, we regard *Neophylloceras* Shimizu 1934, *Paraphylloceras* Shimizu 1935, *Hyporbulites* Breistroffer 1947, *Goretophylloceras* Collignon 1949a, *Euphylloceras* Drushchitz 1953 and *Aphroditiceras* Mahmoud 1956 as synonyms of *Hypophylloceras*. The group thus represents a variable cluster of phylloceratids linked by their apparent common origin in *Phylloceras* of the *serum* group during the early Cretaceous ; detailed study shows that there is every intermediate between the supposedly diagnostic morphologies of the various genera placed in synonymy. Furthermore, the intimate gradational relationship between *P.* (*P.*) *serum* and some *Hypophylloceras* species suggests that even subgeneric separation is more of a stratigraphic convenience than of phylogenetic value.

Occurrence. *Hypophylloceras* has a world-wide distribution, although rare in the boreal region and the western interior of North America. Species first appear in the Valanginian, and range to the Lower Maastrichtian.

1. Group of *P.* (*Hypophylloceras*) *thetys* (d'Orbigny)

This species group is characterized by di- or triphylloid saddles throughout ontogeny. It is thus separable from the *velledae* group where saddles are at first diphylloid, becoming tetraphylloid when adult, and the *seresitense* group where saddles are tetraphylloid throughout ontogeny. The following are referred to the group :

1. *Hypophylloceras thetys* (d'Orbigny) (1841 : 174 ; pl. 53, figs 7–9), Valanginian to Barremian.
2. *Hypophylloceras thetys* (d'Orbigny) *diegoi* Boule, Lemoine & Thévenin (1906 : 10 ; pl. 1, figs 5, 7 ; text-fig. 4), Barremian to Cenomanian.
3. *Hypophylloceras thetys* (d'Orbigny) *majoricense* Wiedmann (1964 : 178 ; pl. 15, fig. 1 ; pl. 18, fig. 3 ; text-fig. 37), Aptian to Albian.
4. *Hypophylloceras sablyense* Karakash (1907 : 39 ; pl. 3, figs 12a–b ; pl. 14, figs 8a–b ; pl. 24, fig. 4), Barremian.
5. *Hypophylloceras fortunei* (Honnorat-Bastide 1892) (Wiedmann 1964 : 192), Aptian.
6. *Hypophylloceras aptiense aptiense* Sayn (1920 : 195 ; pl. 1, fig. 4 ; text-fig. 2), Aptian.
7. *Hypophylloceras aptiense* Sayn *applanatum* Wiedmann (1964 : 190 ; pl. 15, fig. 5 ; text-fig. 43), Aptian.
8. *Hypophylloceras moreti* Mahmoud (1955 : 76 ; pl. 5, figs 2–4 ; text-fig, 44), Albian.
9. *Hypophylloceras aphrodite* Fallot & Termier (1923 : 25 ; pl. 2, figs 5–7 ; text-fig. 5), Albian.
10. *Hypophylloceras subalpinum subalpinum* d'Orbigny (1841 : 283 ; pl. 83, figs 1–3), Albian.
11. *Hypophylloceras subalpinum* d'Orbigny *ellipticum* Kossmat (1895 : 11 ; pl. 1, fig. 2 ; pl. 6, fig. 1), ? Aptian, Albian to Cenomanian.
12. *Hypophylloceras improvisum* (Stoliczka) (1865 : 113 ; pl. 58, figs 4–4b), Cenomanian.
13. *Hypophylloceras subseresitense* Wiedmann (1964 : 202 ; pl. 14, fig. 9 ; pl. 15, fig. 6 ; text-fig. 47), Aptian.
14. *Hypophylloceras sardoum* Wiedmann & Dieni (1968 : 24 ; pl. 1, figs 1, 2 ; pl. 2, fig. 2 ; text-fig. 3), Albian.

Phylloceras (Hypophylloceras) subalpinum (d'Orbigny) **ellipticum** Kossmat

(Figs 2–3 ; Pl. 4, figs 1–4 ; Pl. 5, figs 2–3 ; Pl. 12, fig. 2)

1865 *Ammonites subalpinus* d'Orbigny ; Stoliczka : 114 ; pl. 58, figs 3a–c (non d'Orbigny).
? 1877 *Ammonites velledae* Michelin ; Simonovich, Batsevich & Sorokin : pl. 3, fig. 3 (non Michelin).
1895 *Phylloceras ellipticum* Kossmat : 107 ; pl. 15, figs 2a–b ; pl. 20, figs 1a–b.
non 1897 *Phylloceras ellipticum* Kossmat ; Parona & Bonarelli : 78 ; pl. 10, fig. 7 [= *Phylloceras aphrodite* Fallot & Termier].
1907a *Phylloceras* cf. *ellipticum* Kossmat ; Crick : 169 ; pl. 10, figs 12–12a.
1907 *Phylloceras ellipticum* ? Kossmat ; Pervinquière : 51 ; pl. 3, figs 1, 2a–b ; text-fig. 4.
1910 *Phylloceras ellipticum* Kossmat ; Pervinquière : 10.
1928 *Phylloceras* cf. *ellipticum* Kossmat ; Collignon : 147 ; pl. 1, figs 10–10a.

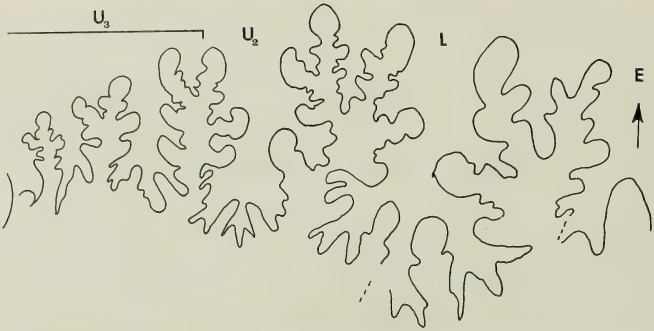


FIG. 2. External suture line of *Phylloceras* (*Hypophylloceras*) *subalpinum ellipticum* Kossmat. SAS A1116, ×6.

1943 *Phylloceras japonicum* Matsumoto : 674 (nom. nud.).
1953 *Phylloceras japonicum* Matsumoto : 147 ; text-fig. 10 (nom. nud.).
non 1956 *Phylloceras* cf. *ellipticum* Kossmat ; Collignon : 15 ; pl. 1, figs 1, 1a, 1b [= *Phylloceras improvisum* (Stoliczka)].
1959 *Partschiceras* ? *japonicum* (Matsumoto) ; Matsumoto : 52 ; pl. 12, figs 1a–c, 2a–b, 3a–c ; pl. 28, figs 2a–d ; pl. 29, figs 1a–b ; text-fig. 2.
1964 *Ph.* (*H.*) *subalpinum ellipticum* Kossmat ; Wiedmann : 197 ; pl. 13, figs 5a–b ; pl. 14, fig. 8 ; pl. 15, figs 3a–c.
1968 *Ph.* (*Hypophylloceras*) *subalpinum ellipticum* Kossmat ; Wiedmann & Dieni : 23 ; pl. 1, fig. 4 ; pl. 2, figs 1a–b.

HOLOTYPE. Kossmat's original specimen from the Utatur Group of southern India (1895 : pl. 15, figs 2a–b ; pl. 20, fig. 1).

MATERIAL. We have fourteen specimens : BM(NH) C18139 (figured by Crick 1907a) probably from the Cenomanian of the Skoenberg region, BM(NH) C78662 from Bed 6, Loc. 51, BM(NH) C78664 from Loc. 54, SAS 2477 and Z38 from Loc. 57, all from the Mzinene River (Albian V) ; BM(NH) C78663 from Bed 4, Loc. 64, BM(NH) C78665, SAS 945, 66/P1 from Loc. 66, Munywana Creek (Albian V), BM(NH) C78666, SAS A499, 10822 and A945 from Loc. 62, the Skoenberg, Mzinene River (Cenomanian II–III) and SAS A1116 from the Albian of the Mzinene (precise horizon unknown). BM(NH) C78686 from Bed 4, Loc. 64, on the Munywana Creek, may also belong here.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (from Kossmat 1895)	71·0	28·5 (40)	41·0 (58)	0·70	5·0 (7)
BM(NH) 78662	45·0	17·8 (40)	25·3 (56)	0·71	3·3 (7)
BM(NH) C78669	58·5	20·0 (34)	35·2 (60)	0·57	3·6 (6)
SAS 10822	56·5	17 (30)	31 (55)	0·55	5·0 (9)
SAS Z447	59·5	20 (34)	35 (59)	0·57	4·0 (7)
SAS 66/P1	56·0	17·5 (31)	31 (55)	0·56	4·5 (8)

DESCRIPTION. The coiling is very involute, with a tiny, funnel-shaped umbilicus (6–9% of diameter). The whorl section is a compressed oval, the whorl breadth to height ratio varying from 0·55 to 0·71, the greatest breadth being typically at or just below mid-flank. The umbilical shoulder slopes gently outwards, producing a funnel-shaped umbilical depression, the flanks being gently inflated, converging to a narrow rounded venter. The surface of the shell is ornamented by low, flat, radial folds which arise at the umbilical seam as mere striae, but strengthen across the lower flank, flexing faintly forwards as they do so, to flex faintly back at mid-flank and pass almost straight across the upper flank and venter. The internal mould is smooth, or bears only faint, low folds.

The suture is moderately subdivided with triphylloid saddles (Figs 2–3).

DISCUSSION. Ornament and whorl section clearly place our specimens close to *P.* (*Hypophylloceras*) *subalpinum ellipticum*; specimens figured as Pl. 5, figs 3a–c and Pl. 6, figs 2a–b have the identical weak fold-like ribs and elliptical whorl section clearly shown in Kossmat's figures and in material illustrated recently by Wiedmann (1964). Other specimens, more compressed than previously-described material referred to this species (whorl breadth to height ratio as low as 0·55) but otherwise identical, we also place within the range of *subalpinum ellipticum*. None of our specimens show the constrictions described by Kossmat, nor the fine striations developed on well-preserved material (e.g. Wiedmann 1964: pl. 15, fig. 3c). The dimensions of *ellipticum* overlap those of *P.* (*H.*) *subalpinum subalpinum*, and involution and sculpture are identical. These similarities led Stoliczka to refer his Indian material to *P.* (*H.*) *subalpinum* s.s. Kossmat, however, separated the Indian material on the basis of the elliptical whorl section with the greatest breadth at or about mid-flank, and the presence of constrictions and fine striations in *ellipticum*, as opposed to the trigonal whorl section in *subalpinum*. As Wiedmann (1964: 198) has noted, no body chambers of *subalpinum* have been described, so that the constrictions and fine striations cannot be used to separate these forms. Whorl section remains as one distinguishing character, while the suture lines of the

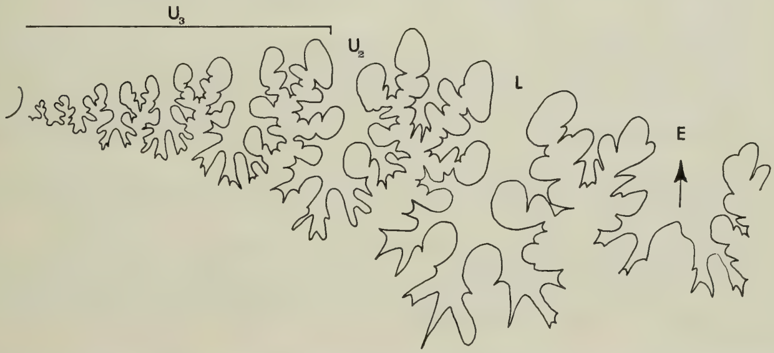


FIG. 3. External suture line of *Phylloceras* (*Hypophylloceras*) *subalpinum ellipticum* Kossmat. SAS Z447, ×3.

present material show that virtually all the saddles are subtriphylloid, thus substantiating Wiedmann's (1964) suggestion that the greatest difference between the two subspecies is in the configuration of the saddles, especially L/U_2.

'*Partschiceras*' *japonicum* Matsumoto, from the Cenomanian of Japan and Alaska, is a clear synonym of *P. subalpinum ellipticum*, whilst the forms compared with this subspecies by Pervinquière (1907, 1910), Crick (1907a) and Collignon (1928) clearly belong to it. The specimen of *Phylloceras* cf. *ellipticum* described by Collignon in 1956 from the Turonian of Madagascar appears to be a *P.* (*Hypophylloceras*) *improvisum* Stoliczka; the *Phylloceras ellipticum* of Parona & Bonarelli (1897) from the Albian of Escragnolles should be referred to *P.* (*Hypophylloceras*) *aphrodite*.

P. (*H.*) *subalpinum ellipticum* is a distinctive form. Whorl section alone readily separates it from *P.* (*H.*) *subalpinum subalpinum*, as noted above, whilst forms such as *P.* (*H.*) *fortunei* and *P.* (*H.*) *sardoum* have distinctly trigonal whorl sections. *P.* (*H.*) *improvisum* is a form with rounded whorls and a broad venter, and *P.* (*H.*) *aptiense aptiense* and *applanatum* and *P.* (*H.*) *aphrodite* all bear constrictions throughout ontogeny. *P.* (*Hypophylloceras*) *thetys thetys*, *thetys diegoi* and *thetys majoricense*, *P.* (*H.*) *moreti* and *P.* (*H.*) *subseresitense* are as readily distinguished, being ornamented by fine striae rather than the low folds of *P.* (*H.*) *subalpinum ellipticum*, and there are other obvious differences (Wiedmann 1964; Wiedmann & Dieni 1968).

Occurrence. *Phylloceras* (*Hypophylloceras*) *subalpinum ellipticum* is known from the Lower Albian of the Balearics, the Upper Albian of Sardinia, Tunisia, southern Russia and South Africa (Zululand), and the Cenomanian of Algeria, southern India, Madagascar, South Africa (Zululand), Alaska and Japan.

Phylloceras (Hypophylloceras) aphrodite Fallot & Termier

(Pl. 3, fig. 3)

1897 *Phylloceras ellipticum* Kossmat; Parona & Bonarelli: 78; pl. 10, fig. 7.
1923 *Phylloceras aphrodite* Fallot & Termier: 25; pl. 2, figs 5–7; text-fig. 5.
1947 *Phylloceras escragnollensis* Breistroffer: 55.
1955 *Salfeldiella* (*Aphroditiceras*) *aphrodite* var. *venus* Mahmoud: 75; pl. 5, fig. 1; text-fig. 43.
1957 *Phylloceras aphrodite* Fallot & Termier; Almela & Revilla: 19; pl. 3, fig. 5.
1957 *Phylloceras* (*Salfeldiella*) *guettardi* Raspail; Almela & Revilla: 16; pl. 2, fig. 6.
1957 *Phylloceras* aff. *grothi* Fallot; Almela & Revilla: 16; pl. 2, fig. 7.
1962a *Hypophylloceras aphrodite* (Fallot & Termier); Wiedmann: 252; pl. 16, fig. 5; text-fig. 5.
1962b *Hypophylloceras aphrodite* (Fallot & Termier); Wiedmann: 141.
1964 *Ph.* (*Hypophylloceras*) *aphrodite* Fallot & Termier; Wiedmann: 184; pl. 18, figs 4–6; pl. 20, fig. 1; text-fig. 40.
1968 *Ph.* (*Hypophylloceras*) *aphrodite* Fallot & Termier; Wiedmann & Dieni: 25.

Neotype. Designated by Wiedmann, 1962a: 252; refigured by him in 1964: pl. 18, figs 4a–c. From the Upper Albian of Son Vida–Son Suredeta, Mallorca (Balearics).

Material. Two specimens. BM(NH) C78667 from Bed 6, Loc. 51 and SAS PJR/1 from Loc. 57, both along the Mzinene River, Zululand (Albian V).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS PJR/1	34·0	14·7 (43)	17·0 (50)	0·87	5·0 (7)
BM(NH) C78667	37·0	16·9 (46)	20·0 (54)	0·84	5·0 (13)

DESCRIPTION. The coiling is very involute, with a small, deep, conical umbilicus (7–13% of diameter). The whorl section is slightly compressed, suboval, with the greatest breadth at mid-flank. The umbilical wall is subvertical, sloping outwards ; the umbilical shoulder is abruptly rounded, the flanks convex and markedly inflated and the venter broadly and evenly rounded. The surface of the test bears fine flexuous striae, and irregular low folds which arise at the umbilical seam, sweep forwards across the inner flank, slightly backwards across mid-flank and forwards again across shoulder and venter. There are four to five deep, narrow, flexuous constrictions per whorl, paralleling the growth striae, which are weak at the umbilical shoulder but deep across the flank and venter. The internal mould is virtually smooth save for constrictions.

The suture includes a rather narrow diphyllic E/L saddle, separated by a trifid lobe from a smaller but also diphyllic L/U_2.

DISCUSSION. The presence of constrictions throughout ontogeny serves to distinguish this species from most other members of the *thetys* group. *P.* (*Hypophylloceras*) *aptiense aptiense* is more compressed (whorl breadth to height ratio is typically 0·7) and has broader, straighter constrictions ; *P.* (*H.*) *aptiense applanatum* has an equally compressed whorl, flat, subparallel flanks and a somewhat flattened venter (Wiedmann 1964 : text-fig. 43a).

OCCURRENCE. Upper Albian of the Balearics, Sardinia, southern France (Escragnolles), Sinai (Moghara Massif) and South Africa (Zululand).

2. Group of *P.* (*Hypophylloceras*) *velledae* (Michelin)

This species group is transitional between the *thetys* and *seresitense* groups, having diphyllic saddles during early ontogeny and tetraphyllic saddles when adult. The following are referred to the group :

1. *Hypophylloceras velledae velledae* (Michelin) (1834 : pl. 35), Albian to Cenomanian.
2. *Hypophylloceras velledae* (Michelin) *morelianum* (d'Orbigny) (1840 : 176 ; pl. 54, figs 1–3), Aptian to Albian.
3. *Hypophylloceras velledae* (Michelin) *aschiltaense* Breistroffer (1947 : 55), Aptian to Albian.
4. *Hypophylloceras velledae* (Michelin) *inflatum* Collignon (1950 : 35 ; pl. 4, figs 16–16b), Albian.
5. *Hypophylloceras ponticuli* (Rousseau) (1842 : 783), Aptian.
6. *Hypophylloceras onoense* Stanton 1895 [= *Ammonites ramosus* Gabb 1864 : 65 ; pl. 11, fig. 12 ; non Meek], Aptian.
7. *Hypophylloceras cypris cypris* Fallot & Termier (1923 : 23 ; pl. 3, figs 1a–c, 2c), Aptian to Albian.
8. *Hypophylloceras cypris* Fallot & Termier *cytherae* Wiedmann (1964 : 218 ; pl. 12, figs 2a–c, 7a–b), Aptian to Albian.

9. *Hypophylloceras pervinquierei* Collignon (1928 : 147, text-fig. 2 ; pl. XV, figs 9, 9a), Lower Cenomanian.

Phylloceras (Hypophylloceras) velledae (Michelin)

This is the most commonly cited Albian phylloceratid, and the most frequently misinterpreted. Wiedmann (1964 : 205–207) has now clarified much of the confusion surrounding the species, and has designated a neotype for the restricted form. The species can be subdivided as follows :

1. Whorl section compressed, oval, maximum whorl breadth at umbilical wall, sides flat – *P.* (*H.*) *velledae morelianum* (d'Orbigny), Aptian ? to Albian.
2. Whorl section compressed, oval, sides moderately inflated, greatest breadth on inner third of flanks – *P.* (*H.*) *velledae velledae* (Michelin), Albian to Cenomanian.
3. Whorl section compressed, elliptical, flanks inflated, greatest breadth at mid-flank – *P.* (*H.*) *velledae aschiltaense* Breistroffer, Aptian to Albian.
4. Whorl section subcircular, maximum whorl breadth on inner third of strongly rounded flanks – *P.* (*H.*) *velledae inflatum* Collignon, Albian.

Phylloceras (Hypophylloceras) velledae velledae (Michelin)

(Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 ; Pls 8, 10, 11)

1834 *Ammonites velledae* Michelin : pl. 35.
1841 *Ammonites velledae* Michelin ; d'Orbigny : 280 ; pl. 82, figs 1–4.
1907b *Phylloceras* sp. Crick : 236.
1921a *Phylloceras velledae* (Michelin) ; Spath : 273.
1925 *Phylloceras velledae* (Michelin) ; Spath : 181–182.
1928 *Phylloceras velledae* (Michelin) ; Collignon : 6 ; pl. 1, figs 1–1a.
1930 *Phylloceras velledae* (Michelin) ; Besairie : 212 ; pl. 17, fig. 2.
1936 *Phylloceras velledae* (Michelin) ; Venzo : 66 ; pl. 5, figs 4a–b.
1947 *Phylloceras velledae* (Michelin) ; Breistroffer : 55.
1949a *Phylloceras velledae* (Michelin), var. ; Collignon : 44 ; pl. 7, figs 1–1a ; text-figs 4, 5.
1960 *Euphylloceras velledae* Michelin ; Drushchitza & Kudryavtseva : 252 ; pl. 2, figs 5a–b.
1962a *Hypophylloceras velledae velledae* (Michelin) ; Wiedmann : 250 ; pl. 16, fig. 4.
1962b *Hypophylloceras velledae velledae* (Michelin) ; Wiedmann : 142.
1963 *Phylloceras velledae* (Michelin) ; Collignon : 4 ; pl. 241, figs 1036.
1964 *Phylloceras velledae* (Michelin) ; Collignon : 4 ; pl. 318, fig. 1347.
1964 *Phylloceras* (*Hypophylloceras*) *velledae velledae* (Michelin) ; Wiedmann : 209 ; pl. 11, figs 1a–c ; pl. 13, figs 4a–b ; pl. 21, figs 4a–b ; text-fig. 49. (With full synonymy.)
1968 *Ph.* (*Hypophylloceras*) *velledae velledae* (Michelin) ; Wiedmann & Dieni : 25 ; pl. 1, figs 5a–b.

NEOTYPE. Designated by Wiedmann, 1964 : 211. MHNP 1895–17 (d'Orbigny Collection) from the Albian of Épothémont, near Bar-sur-Aube, Aube, France.

MATERIAL. Numerous specimens. SAS LJE 86 from Loc. 163, Mfongosi Creek (Aptian III) ; BM(NH) C78685 from Loc. 36 on the Mzinene River (Albian III) ; BM(NH) C78668 from Bed 1 at Loc. 51, on the Mzinene (Albian IV) ; BM(NH) C78677, C78670 and C78683 from Bed 6, C78684, C78682 from Beds 12–13 and BM(NH) C78669 (loose) also from Loc. 51 (Albian V); BM(NH) C78678, ? C78679, SAS Z1503, Z1491, Z1492a–b, from Loc. 54 on the Mzinene; BM(NH) C78671–6 from Loc. 56 on the Mzinene; SAS A1847, from Loc. 57 on the Mzinene; all Albian V. SAS A2053, PJR/2, Z1195, Z564, Z1248, Z1247 from Loc. 64; SAS 26/3214, 26/3227, 26/3223, BM(NH) C78680–1 and C78689 from Loc. 65, and SAS A1189 from Loc. 66, all on the Munywana (Albian V). SAS Z17(5), Z17(6) and Z19a–b come from Haughton's (1936 : 291; fig. 3) localities 17 and 19 in northern Zululand.

The specimen referred to by Spath (1921a : 273) from the 'Middle Branch of the Manuan Creek', SAM 4992, also belongs to this species, as does Crick's (1907b) *Phylloceras* sp., BM(NH) C18264.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Neotype	165·0	61·0 (37)	98·0 (59)	0·62	—
Collignon 1949b : 45	118·0	44·0 (37)	69·0 (59)	0·63	5 (4)
Collignon 1963 : 4	114·0	43·0 (38)	68·0 60)	0·63	3 (3)
SAS 3214	99·7	37·0 (37)	57·2 (57)	0·65	6·0 (6)
SAS Z19	117·2	40·0 (35)	70·0 (60)	0·57	5·5 (5)
SAS Z17 (5)	137·5	47·7 (35)	83·2 (60)	0·57	6·8 (5)
SAS Z1492a	162·0	55·0 (34)	97·2 (60)	0·57	6·5 (4)
SAS Z1496	169·0	60·2 (36)	103·2 (61)	0·60	9·5 (6)
BM(NH) C78668	208·0	77·5 (37)	121·0 (58)	0·63	11·5 (6)

DESCRIPTION. The coiling is involute, with a tiny umbilicus, 3–7% of the diameter, with an outwards sloping wall. The whorl section is compressed, the whorl breadth to height ratio varying from 0·55 to 0·63, with the greatest breadth well below mid-flank. The sides are gently rounded, and converge from the lower flanks towards a quite broad, rounded venter. Ornament consists of fine flexuous striae, hair-like around the umbilicus, but coarsening and flattening on the upper flank and venter where they are approximately as wide as the interspaces; there are about two hundred per whorl. They sweep gently forwards across the inner flank, backwards across mid-flank, and then forwards across the upper flank to pass across the venter with a shallow forward projection. There are no constrictions nor do the striae bunch. Internal moulds bear traces of the same ornament as the shell surface.

The suture of large specimens includes an asymmetrically diphyllic saddle E/L, separated by a trifid lateral lobe from an L/U_2 saddle, with five folioles (Pl. 6, fig. 3a).

DISCUSSION. Wiedmann gives a complete synonymy for this form, and demonstrates very clearly how few of the specimens referred to *Phylloceras velledae* actually belong to the restricted species. Our collections contain, however, a large number of specimens ranging from juveniles to individuals which are still wholly septate at diameters of over 200 mm and match the neotype in proportions, style of ornament and suture. There is some variation in relative proportions and in strength of ornament, but all the material belongs to a single form. Our material appears to be the largest described collection of *P.* (*H.*) *velledae velledae*, and an ontogenetic series and a number of adult variants are figured here.

Differences between *P.* (*Hypophylloceras*) *velledae velledae, morelianum, aschiltaense* and *inflatum* have already been given. The other Albian members of this group, *P.* (*H.*) *cypris cypris* and *P.* (*H.*) *cypris cytherae*, both show distinctly fasciculate ornament ; the former has a subtrigonal whorl section, and both have a more open umbilicus.

P. (*Hypophylloceras*) *seresitense*, the other species of *Hypophylloceras* represented by large individuals in our collections, has a much wider umbilicus, and has much finer, straighter striae at similar diameters.

OCCURRENCE. Lower Albian of the Balearics ; Upper Albian of France ; Middle Aptian and Upper Albian of South Africa ; Upper Albian of Mozambique ; Lower Albian to Cenomanian of Madagascar.

Phylloceras (Hypophylloceras) velledae (Michelin) ***inflatum*** Collignon

(Pl. 13, fig. 1)

1950 *Phylloceras velledae* Michelin var. *inflata* Collignon : 35 ; pl. 4, figs 16–16b.
1962a *Phylloceras velledae inflatum* Collignon ; Wiedmann : 142.
1963 *Phylloceras velledae* Michelin var. *inflata* Collignon : 6 ; pl. 242, fig. 1040.
1964 *Phylloceras velledae inflatum* Collignon ; Wiedmann : 207.

LECTOTYPE. The specimen figured by Collignon (1950) as his pl. 4, figs 16–16b, from the Lower Albian of Komihevitra, Madagascar, is herein designated lectotype.

MATERIAL. One specimen only, SAS 1742, from the Middle or Upper Albian of the Mzinene River, Zululand.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Lectotype	98·0	49·0 (50)	58·0 (59)	0·84	2·0 (2)
Collignon 1963 : 6	104·0	52·0 (50)	64·0 (62)	0·81	4·0 (4)
SAS 1742	81·0	40·0 (50)	45·3 (56)	0·88	4·0? (5?)

DESCRIPTION. The coiling is very involute, with a tiny, occluded umbilicus. An outward-sloping umbilical shoulder produces a conical circumbilical depression. The whorl section is subrounded, the whorl breadth to height ratio being 0·88. The whorl sides are inflated and the venter broadly rounded ; the greatest breadth is close to the umbilical shoulder. Ornament consists of fine, dense, flexuous striae, weak on the lower flank, but strong on the upper flanks and venter. The striae arise at the umbilical seam, pass straight across the lower flank, flex gently backwards at mid-flank, and gently forwards across shoulders and venter. The internal mould bears weaker but otherwise similar ornament.

DISCUSSION. The occluded umbilicus, whorl section and ornament clearly place this specimen in *P.* (*Hypophylloceras*) *velledae inflatum* ; it is identical with the Malagasy material figured by Collignon, save for slight differences in relative proportions. This form is readily distinguished from other subspecies of *velledae*, none of which approaches its degree of inflation. Form of umbilicus and ornament, as well as inflation, clearly differentiate it from other members of the *velledae* group.

Occurrence. Lower Albian of Madagascar; Middle or Upper Albian of South Africa (Zululand).

Phylloceras (Hypophylloceras) sp. aff. **velledae** (Michelin)

(Pl. 5, fig. 1; Pl. 7, fig. 1)

cf. 1972 *Hypophylloceras* aff. *californicum* (Anderson); McLearn: 22; pl. 1, figs 1a–b, 2a–b.

Material. Three specimens: BM(NH) C78696, from Loc. 51, collected loose but of Upper Albian age; BM(NH) C78695 from Loc. 56; SAS A2239 from Loc. 57; all Mzinene River, Zululand (Albian V).

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78695	81·8	31·0 (38)	46·5 (57)	0·66	5·0 (6)
BM(NH) C78696	107·5	43·5 (40)	64·2 (59)	0·67	7·2 (6)
SAS A2239	147·4	—	89·5 (60)	—	9·1 (6)

Description. Three specimens in our collection appear to belong to the *velledae* group, but differ from *P.* (*H.*) *velledae velledae* in having a broader whorl section and from *velledae velledae* and *velledae inflatum* in their coarser ornament, effaced on the inner flank and not obviously flexuous. McLearn has recently figured (1972: pl. 1, figs 1–2, especially 2) similar specimens from the Lower Albian of the Queen Charlotte Islands, British Columbia, referring to them as *Hypophylloceras* aff. *californicum* (Anderson). The type of this species is, however, a finely ornamented form, known only as a fragment from the Lower Albian of California (Anderson 1938: 143; pl. 12, fig. 7) and which is too poorly described and figured for adequate comparisons.

Occurrence. Upper Albian of Zululand. Lower and Upper Albian of the Queen Charlotte Islands, British Columbia.

3. Group of *P.* (*Hypophylloceras*) *seresitense* Pervinquière

This group, characterized by possession of tetraphylloid saddles even in the early stages, includes seven Lower Cretaceous forms, most of which are listed by Collignon (1956: 29 et seq.). Included here are the *Neophylloceras*, *Epiphylloceras* and *Hyporbulites* of previous workers.

Phylloceras (Hypophylloceras) seresitense Pervinquière

The species can be divided as follows (Wiedmann 1964: 221).

1. Whorl section moderately compressed, whorl breadth to height ratio up to 0·65, umbilicus narrow – *P.* (*H.*) *seresitense seresitense* Pervinquière, Aptian to Cenomanian.
2. Whorl section very compressed, whorl breadth to height ratio 0·50–0·57, umbilicus narrow – *P.* (*H.*) *seresitense boulei* Collignon, Albian to Cenomanian.
3. Whorl section high, umbilicus moderately open – *P.* (*H.*) *seresitense tanit* Pervinquière, Albian to Cenomanian.

Phylloceras (Hypophylloceras) seresitense seresitense Pervinquière (Pl. 4, fig. 6 ; Pl. 6, fig. 4 ; Pl. 7, fig. 4 ; Pl. 9)

1865 *Ammonites velledae* Michelin ; Stoliczka : 116 ; pl. 59, fig. 1.
1895 *Phylloceras velledae* Michelin ; Kossmat : 12 ; pl. 1, fig. 3.
1907 *Phylloceras velledae* var. *seresitense* Pervinquière : 52.
1907a *Phylloceras velledae* Michelin ; Crick : 166 ; pl. 10, figs 10–11.
1910 *Phylloceras velledae* var. *seresitensis* Pervinquière ; Pervinquière : 9, text-fig. 2 ; pl. 1, figs 1–3.
non 1923 *Phylloceras seresitense* Pervinquière ; Spath : 18 ; pl. 1, fig. 2 ; pl. 2, fig. 1 [= *P. seresitense tanit* Pervinquière].
? 1928 *Phylloceras* ex aff. *ramosi* Meek ; Collignon : 1 ; pl. 1, figs 2–4.
? 1936 *Phylloceras seresitense* Pervinquière ; Collignon : 190 ; pl. 21, figs 1–2.
1940 *Phylloceras seresitense* Pervinquière ; Fabre : 211 ; pl. 5, fig. 1.
1943 *Phylloceras velledae* Michelin ; Matsumoto : 676.
1947 *Hyporbulites seresitensis* Pervinquière ; Breistroffer : 82.
1950 *Phylloceras* (*Hyporbulties*) *seresitense* Pervinquière ; Collignon : 66.
1956 *Hyporbulites seresitensis* var. *raynaudiensis* Collignon : 16 ; pl. 4, fig. 1.
1959 *Neophylloceras seresitense* (Pervinquière) ; Matsumoto : 55, text-fig. 3 ; pl. 12, figs 4–5.
1962a *Hypophylloceras seresitense seresitense* (Pervinquière) ; Wiedmann : 142, text-fig. 8 ; pl. 8, figs 1–2.
1962b *Hypophylloceras seresitense seresitense* (Pervinquière) ; Wiedmann : 249 ; pl. 16, fig. 1.
1963 *Phylloceras* (*Hyporbulites*) *seresitensis* Pervinquière ; Collignon : 4 ; pl. 241, fig. 1038 ; pl. 142, fig. 1041.
1964 *Ph.* (*Hypophylloceras*) *seresitense seresitense* Pervinquière ; Wiedmann : 221 ; pl. 15, figs 4a–b ; pl. 21, figs 1a–b ; text-fig. 52.
1968 *Phylloceras* (*Hypophylloceras*) *seresitense seresitense* Pervinquière ; Wiedmann & Dieni : 26.

Lectotype. The original of Pervinquière 1910 : pl. 1, fig. 1, designated by Wiedmann (1964).

Material. Four specimens : BM(NH) C78690, C18137–8 from the Skoenberg (? Cenomanian III), and SAS A1401 from Loc. 36 on the Mzinene River (Albian III), all from Zululand.

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C18138	28·3	10·6 (37)	16·7 (59)	0·64	1·5 (5)
SAS A1401	190·0	69·3 (36)	109·2 (57)	0·63	10·5 (5)

Description. Our specimens add nothing to knowledge of the early development of this species, which is well known. We have, however, a near adult specimen (SAS A1401, Pl. 9) still wholly septate at 190 mm, which appears to be the largest known individual referred to it. The coiling is very involute, the umbilicus small, conical and deep (5% of diameter) with a rounded undercut wall and an outwards sloping shoulder which merges with the flanks. The whorl section is compressed, the greatest breadth being one-third of the way up the flanks. The sides are gently inflated, converging to a broad rounded venter.

Ornament consists of dense, fine striae, flat-topped, and as wide as the interspaces. There are between 400 and 450 of these on the outer whorl. They arise at the umbilical seam and are very faint, but strengthen across the flanks. They flex gently forwards on the inner flank, backwards over the outer flank and forwards across the shoulders to pass straight across the venter. The major saddles of the suture (E/L and L/U_2) are tetraphylloid.

Discussion. Our smaller specimens, originally figured by Crick as *Phylloceras velledae* Stoliczka (? Michelin), clearly belong to *P.* (*H.*) *seresitense seresitense*, as indicated by Wiedmann (1964). Our adult specimen, still wholly septate at a diameter of 190 mm, is referred to *P.* (*Hypophylloceras*) *seresitense* on the basis of the style and strength of ornament, relative proportions and such of the suture line as is visible. The whorl breadth to height ratio clearly excludes reference to *P.* (*H.*) *seresitense boulei*, but separation from *P.* (*H.*) *seresitense tanit* cannot be definitely confirmed at this size because the largest described *tanit* has a diameter of only 62 mm. It seems, however, that the umbilicus of *tanit* is usually 10% or more of the diameter.

Occurrence. *P.* (*Hypophylloceras*) *seresitense seresitense* ranges from the Upper Aptian (Balearics) to the Cenomanian. The geographic distribution includes southern France, northern Spain, north Africa, the Balearics, southern India, Madagascar, South Africa and Alaska.

Phylloceras (Hypophylloceras) androiavense Besairie

(Pl. 4, fig. 7)

1936 *Phylloceras androiavensis* Besairie : 165 ; pl. 16, figs 9–11.
1963 *Phylloceras* (*Hyporbulites*) *androiavense* Besairie ; Collignon : 4 ; pl. 241, fig. 1037.

Lectotype. Besairie's figured specimen (1936 : pl. 16, figs 9–11), from the upper part of the Middle Albian of Androiavy, Madagascar, is herein designated lectotype.

Material. One specimen only, BM(NH) C78667, from Loc. 54, Mzinene River, Zululand (Albian V).

Description. Our specimen is fragmentary, with an original diameter of approximately 40 mm. The coiling is very involute, with a tiny umbilicus (approximately 5% of the diameter). The whorl section is very compressed (whorl breadth to height ratio about 0·46), the greatest breadth being at the umbilical shoulder. The whorls are rapidly expanding, the whorl height being approximately 60% of the total diameter. The umbilical shoulder is quite abruptly rounded, the sides flat and subparallel with a narrow rounded venter. Ornament consists of fine, flexuous striae grouped into bunches ; about ten low, fold-like ribs arise at the umbilical shoulder, pass forwards across the inner flank, and flex backwards at mid-flank where they give rise to numerous striae which sweep gently forwards across the shoulder and venter, together with similar intercalated striae. The inner flanks between folds bear fine irregular striae. The sutures are not exposed.

Discussion. Our specimen is identical in style of ornament, whorl section and (as far as can be determined) relative proportions to *P.* (*Hypophylloceras*) *androiavense*. Apart from this species, fasciculate ornament is present in the following mid-Cretaceous forms. *P.* (*Hypophylloceras*) *cypris cypris* Fallot & Termier (1923 : 22; pl. 3, figs 1a–c, 2c) is an Albian form, differing, however, in having a subtrigonal whorl section, a whorl breadth to height ratio of 0·66, and a larger umbilicus 12% of the diameter. *P.* (*Hypophylloceras*) *cypris cytherae* Wiedmann (1964 : 218; pl. 12, figs 2a–b, 7a–b; pl. 15, fig. 8a–b; text-fig. 12) is an Upper Aptian to Albian form with a compressed, oval whorl section, rounded flanks, a whorl breadth to height ratio of 0·66 and a larger umbilicus 12% of the diameter. *Hypophylloceras algeriense* Wiedmann (1962 : 144; pl. 8, fig. 3a–b; text-fig. 9), an Albian to Cenomanian species with a whorl breadth to height ratio of 0·65, has rounded, convergent flanks and an arched venter.

OCCURRENCE. High Middle Albian of Madagascar; Upper Albian of South Africa (Zululand).

Phylloceras (Hypophylloceras) woodsi woodsi van Hoepen

(Figs 4–6; Pl. 13, figs 3–5)

1906 *Phylloceras* sp., Woods : 331; pl. 41, fig. 4.
1921 *Phylloceras woodsi* van Hoepen : 3; pl. 2, figs 1–6; text-fig. 1.
1921b *Phylloceras nera* (Forbes); Spath : 40.
1922 *Phylloceras woodsi* van Hoepen; Spath : 117.
1929 *Phylloceras woodsi* van Hoepen; Barrabé : 174; pl. 9, fig. 17.
1930 *Phylloceras woodsi* van Hoepen; Besairie : 567 (223); pl. 21, figs 2–2a.
1931 *Phylloceras woodsi* van Hoepen; Collignon : 10.
1956 *Hyporbulites woodsi* van Hoepen; Collignon : 19.
1956 *Hyporbulites hoepeni* Collignon : 19; pl. 1, figs 4, 4b, 5, 5b, 6–6b; text-fig. 4.
1966 *Phylloceras* (*Hyporbulites*) *hoepeni* Collignon; Collignon : 1; pl. 455, fig. 1406.

HOLOTYPE. TM 537, figured by van Hoepen (1921 : pl. 2, figs 3–4).

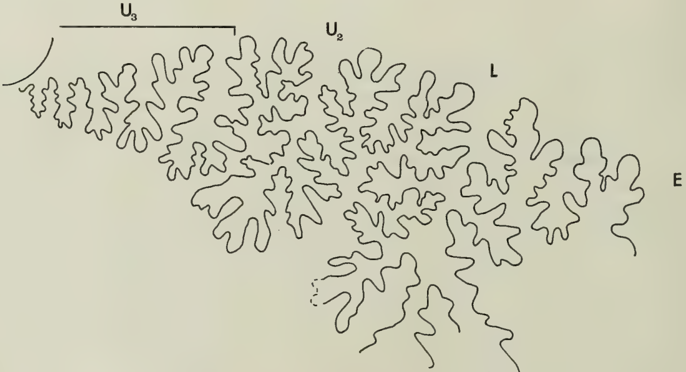


FIG. 4. External suture line of *Phylloceras* (*Hypophylloceras*) *woodsi woodsi* van Hoepen. Holotype, TM 537, × 12·5.

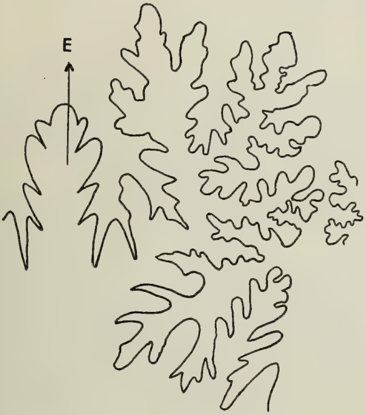


FIG. 5. Partial external suture of *Phylloceras* (*Hypophylloceras*) *woodsi woodsi* van Hoepen. TM 529, ×6.

MATERIAL. Eight specimens: the holotype TM 537; four paratypes, TM 529, 530, 533, 534; a specimen in the Durban Museum (unregistered); a specimen in the Griesbach Collection, figured by Woods (1906); and BM(NH) C78826. All are from the Umzamba Formation of Loc. 1, Umzamba, Pondoland, and are of Santonian or Campanian age.

DESCRIPTION. The coiling is moderately involute (umbilicus approximately 7–10% of diameter). The whorl section is a compressed oval with virtually parallel flanks, converging only slightly towards the gently rounded venter. Maximum whorl width is at the middle to inner third of the flanks. The umbilicus is pit-like, with nearly vertical walls, thus forming a pronounced, angular umbilical shoulder.

Ornament consists of numerous, fine single ribs which are most pronounced on the outer third of the flanks. Ribbing on the inner third is very faint, but the ribs appear to originate at the umbilical edge, flex slightly backward on the inner third of the flanks and gently forward at mid-flank, and then pass in a prorsiradiate direction across the ventrolateral shoulders.

The suture is typically phylloid on the inner whorls, but tends to become more dendritic at the largest diameters studied. E/L is diphylloid, separated from the triphylloid L/U_2 by a trifid lateral lobe.

DISCUSSION. Collignon (1956: 19), when erecting *P.* (*H.*) *hoepeni*, stated that the species was very close to *P.* (*H.*) *woodsi*; as far as relative proportions are concerned, the two species overlap to a great extent. *P.* (*H.*) *hoepeni* has a smaller umbilicus than the present species, 3–6% of diameter as against 7–10% in *P.* (*H.*) *woodsi*, but Collignon realized that this criterion is difficult and rather impracticable to apply. He stated, in addition, that the suture lines were different; in *P.* (*H.*) *hoepeni* the suture line is more zigzag-like and the saddles have smaller stems and are more incised. Unfortunately, only E/L and part of the lateral lobe of *P.* (*H.*) *hoepeni* have been figured by Collignon (reproduced here as Fig. 6), whilst the suture line given by van Hoepen for *P.* (*H.*) *woodsi* is rather schematic.

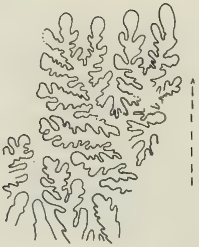


Fig. 6. Partial external suture line of *'Hyporbulites' hoepeni* Collignon (= *P.* (*Hypophylloceras*) *woodsi woodsi* van Hoepen herein), after Collignon (1956 : text-fig. 4), ×4·5.

Virtually the same part of the suture line as figured by Collignon is visible on one of the paratypes of *P.* (*H.*) *woodsi*, TM 529 (Fig. 5) ; it is quite clear that, apart from the folioles in the saddles of *P.* (*H.*) *hoepeni* being more phylloid than in *P.* (*H.*) *woodsi*, the two suture lines are identical. Because of the comparable relative proportions, similar suture lines and (probably) the same stratigraphic occurrence, *P.* (*H.*) *hoepeni* is here regarded as a junior synonym of *P.* (*H.*) *woodsi*. *P.* (*H.*) *hoepeni infundibuliformis* Collignon is also referred to *P.* (*H.*) *woodsi* as a subspecies. It is more inflated than the nominal subspecies and stands in the same relationship to *P.* (*H.*) *woodsi* that *P.* (*H.*) *subalpinum ellipticum* does to *P.* (*H.*) *subalpinum subalpinum*.

Less readily resolved is the relationship of *P.* (*H.*) *woodsi* to *'Neophylloceras' marshalli* Shimizu [= *Phylloceras nera* Marshall (non Forbes) 1926 : 124 ; pl. 19, fig. 4 ; pl. 26, figs 1–2], *'N.' hetonaiense* Matsumoto (1943 : 675, text-figs $1a_3$, b_3) of which *'N.' lambertense* Usher (1952 : 50 ; pl. 1, figs 1–3) is a synonym (Jones 1963 : 23), and *'N.' nera* Forbes (1846 : 106 ; pl. 8, fig. 7). All have ornament well within a range of intraspecific variation which we would find acceptable in phylloceratids. In the suture line of *N. hetonaiense*, however, the elements of the suspensive lobes form a concave arc ; in *N. nera* they lie on a straight line, and in the present species the suspensive lobe is slightly retracted (Fig. 4). Given better collections, it may be possible to show that all these species are junior subjective synonyms of *P.* (*Hypophylloceras*) *nera*.

Occurrence. Santonian or Campanian of Zululand; Santonian *Texanites oliveti* Zone, Madagascar.

Phylloceras (Hypophylloceras) mikobokense (Collignon)

(Pl. 12, fig. 1)

1938 *Phylloceras* aff. *surya* (Forbes) ; Collignon : 41 ; pl. 7, fig. 1.
1956 *Epiphylloceras mikobokense* Collignon : 24 ; pl. 2, figs 3–3a ; pl. 4, figs 5–5b.

Holotype. MNHP 1567, figured by Collignon (1956 : pl. 4, figs 5–5b), from the Lower Maastrichtian of Lajona, Madagascar.

Material. Two specimens, SAS H163c/7 and 163/9, from Loc. 20, Mfolozi River, Zululand (Maastrichtian I).

DIMENSIONS. (From Collignon 1956 : 24)

	D	Wb	Wh	Wb/Wh	U
EMP 1567	86·0	25·0 (29)	42·0 (49)	59	—
EMP 1564	73·0	23·0 (32)	42·0 (58)	55	11·0 (15)

DESCRIPTION. Our specimens are fragments of discoidal shells with a moderately high expansion rate and a compressed whorl section (whorl breadth to height ratio is 0·51), the greatest breadth being close to the umbilical shoulder. The umbilicus is small, about 10% of the inferred diameter, quite deep, with a subvertical, rounded wall and an abruptly rounded shoulder. The flanks are rounded, converging to a narrowly rounded venter.

Ornament consists of fasciculate ribs and striae. Our specimens bear strong fold-like ribs which arise at the umbilical seam, pass straight across the lower flank, thicken and flex backwards across the outer flank, and die out across the ventrolateral shoulder, being represented on the venter merely by low, broad swellings. Superimposed on these are fine, dense striae, arising at the umbilical seam, branching on the flanks and following a course parallel to the ribs.

The suture is deeply incised, having lost the typical phylloid terminations (Pl. 14, fig. 1b).

DISCUSSION. The very coarse, fold-like ribs and fine striae, and relative proportions, indicate that our specimens belong to Collignon's species, comparing closely with the large paratype fragment figured by him (1956 : pl. 2, figs 3–3a). Ornament readily separates this species from most Upper Cretaceous *Hypophylloceras*, whilst those forms with comparable fasciculate ornament ('*Epiphylloceras*' of authors) differ as follows. *Hypophylloceras surya* (Forbes) (1846 : 106 ; pl. 7, fig. 10) has much coarser ribbing rather than striae ; *Hypophylloceras cottreaui* Collignon (1956 : 25 ; pl. 4, figs 6a–b) lacks strong fold-like ribs, having instead fasciculate striae arising from umbilical bullae. *Epiphylloceras radiatum* Marshall (1926 : 135 ; pl. 19, fig. 7 ; pl. 26, figs 3–4 ; see also Henderson 1970 : 6, text-fig. 26) has a smaller umbilicus and less compressed whorls, the whorl breadth to height ratio being 0·72.

OCCURRENCE. Lower Maastrichtian of Madagascar and South Africa (Zululand).

Genus ***PARTSCHICERAS*** Fucini 1920

TYPE SPECIES. *Ammonites partschi* Stur 1851 (non Klipstein 1843), by the subsequent designation of Spath, 1927.

DISCUSSION. This genus is reviewed at length by Wiedmann (1962b : 257 ; 1964 : 229). Our material is too poor to allow profitable discussion, and we have therefore followed him in regarding *Phyllopachyceras* Spath 1925, *Procliviceras* Fucini 1920, *Macrophylloceras* Spath 1927, *Hoplophylloceras* Spath 1927, *Partchiphylloceras* Roman 1938 and ? *Calaiceras* Kovacs 1939, as synonyms.

OCCURRENCE. Sinemurian to Maastrichtian ; in the Cretaceous species have a world-wide distribution save for the boreal region of north-west Europe and the western interior of North America.

Partschiceras umzambiense (van Hoepen)

(Fig. 7 ; Pl. 13, fig. 2)

1920 *Phylloceras umzambiense* van Hoepen : 142 ; pl. 24, figs 1–3.
1921b *Phylloceras umzambiense* van Hoepen ; Spath : 50.
1922 *Phylloceras umzambiense* van Hoepen ; Spath : 117.
1956 *Phyllopachyceras umzambiense* (van Hoepen) ; Collignon : 27 ; pl. 2, figs 2–2b ; text-fig. 8.
1966 *Phyllopachyceras umzambiense* (van Hoepen) ; Collignon : pl. 455, fig. 1850.

HOLOTYPE. TM 524, figured by van Hoepen (1920 : pl. 24, figs 1–3), from the Umzamba Formation, Loc. 1, Pondoland, and of Santonian–Campanian age.

MATERIAL. The holotype only.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
TM 524	44·0	17·0 (39)	27·0 (61)	0·63	2·0 (5)
EMP 1587 (Collignon 1956)	22·0	10·0 (45)	13·0 (59)	0·76	1·0 (5)
Collignon 1966 : pl. 455, fig. 1850	21	10·0 (49)	12 (57)	0·83	1·0 (9)

DESCRIPTION. The holotype is an incomplete, septate internal mould, badly abraded on one side. Coiling is involute with a small umbilicus, 5% of the diameter. The umbilicus is funnel-shaped and not distinctly demarcated from the flanks. Whorl section is ovoid with rounded flanks and a broad venter. Maximum breadth is at the inner third of the whorl.

Ornament consists of thin, sinusoidal ribs, separated by somewhat wider interspaces. The ribs flex forwards on the inner half of the flanks and then backwards on the outer half to traverse the venter radially. Approximately eight pairs of fasciculate ribs arise at the umbilicus as low, radial swellings which are confined to the umbilicus, disappearing on the flanks. Apart from the normal ribs, intercalatories or bifurcating ribs originate at about mid-flank.

The main saddles (E/L and L/U_2) are tetraphyllic. L is larger than U_2 (Fig. 7).

DISCUSSION. This is a relatively rare species and has only been recorded on three occasions to date (van Hoepen 1921 ; Collignon 1956, 1966). The main distinguishing feature is the ornamentation of fasciculate ribbing near the umbilicus and intercalatory bifurcating ribbing on the vental part of the flanks.

Partschiceras besairiei besairiei Collignon and *P. besairiei tsianalokensis* (Collignon 1931 : 10 ; pl. 1, figs 2–2b, 3–3a, 4–4b ; pl. 8, fig. 1) from the Santonian of Madagascar bear a superficial resemblance as far as inflation of the whorls is concerned, but has different ornamentation ; *P. besairiei besairiei* has strong ribs on the ventral area and *P. besairiei tsianalokensis* lacks ribbing altogether. Of other Upper Cretaceous species, *Parschiceras forbesianum* (d'Orbigny 1850 : 213) (of which according to Henderson (1970 : 7) *P. ezoense* Yokoyama (1890 : 170 ; pl. 19, figs 2a–c), *P. minimum* Marshall (1926 : 137 ; pl. 19, fig. 8 ; pl. 26, figs 5–6), *P. bistriatum* Marshall (1926 : 138 ; pl. 19, fig. 5 ; pl. 27, figs 1–2), *P. inflatum* Shimizu (1935 : 178), *P. marshalli* Collignon (1937 : 26) and *P. zelandicum* Collignon (1956 : 31) are synonyms), *P. whiteavesi* Kossmat (1897 : 124–125 [= *Phylloceras forbesianum*

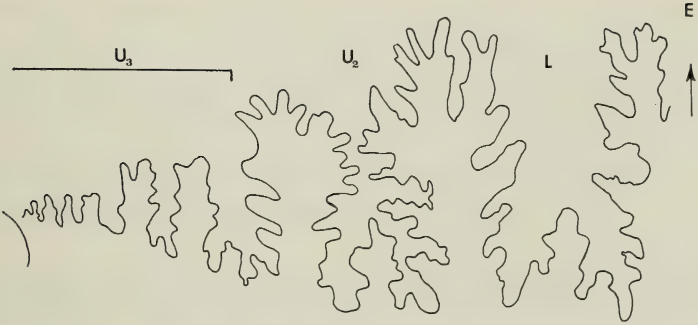


FIG. 7. External suture line of *Partschiceras umzambiense* (van Hoepen). Holotype, TM 524, ×6.

Kossmat (non d'Orbigny) 1895 : 109 ; pl. 15, figs 1a–c ; = *Ammonites rouyanus* Stoliczka (non d'Orbigny) 1865 : 117 ; pl. 69, figs 5–7]) and *P. occlusum* Tate (1865 : 36 ; pl. 3, figs 1a–b) all lack the fine, dense, wiry ribbing of *P. umzambiense* and are virtually smooth when preserved as internal moulds. '*Epiphylloceras*' species, which may bear similar fasciculate ribbing, all differ from *P. umzambiense* in their compressed whorl section.

OCCURRENCE. Santonian of Madagascar (*Texanites oliveti* Zone) ; Santonian or Lower Campanian of Pondoland.

Partschiceras sp. juv. ? cf. ***baborense*** (Coquand)

(Pl. 6, figs 2–3)

cf. 1880 *Ammonites baborensis* Coquand : 26.
cf. 1964 *Partschiceras baborense* (Coquand) ; Wiedmann : 243 ; pl. 14, figs 2, 4, 5 ; pl. 16, figs 1–2 ; pl. 21, figs 5, 6 ; text-fig. 59. (With synonymy.)

MATERIAL. Three specimens, BM(NH) C78692–4, from Loc. 170, Mlambongwenya Spruit, northern Zululand (Barremian I).

DIMENSIONS.	*D*	*Wb*	*Wh*	*U*
BM(NH) C78693	18·0	— (—)	10·1 (56)	—

DESCRIPTION. The shell is involute, with an occluded umbilicus. The whorls are slightly compressed, the greatest breadth being close to mid-flank. Although the umbilicus is occluded, the umbilical wall slopes outwards to produce a shallow conical circumbilical pit before merging with the broadly rounded, subparallel flanks. The ventrolateral shoulder and venter are broadly and evenly rounded. The shell surface is quite without ornament, although this may be a result of partial decortication.

The suture is too poorly exposed and corroded for detailed description.

DISCUSSION. These specimens are too poor for satisfactory determination. The nature of the umbilicus, lack of ornament and relative proportions recall, however, *Partschiceras baborense*, especially pyritic juveniles figured by Wiedmann (1964) and Collignon (1937 : pl. 1, figs 4–4b to 6–6b).

OCCURRENCE. *P. baborense* ranges from Barremian to Aptian, and occurs widely in southern France, northern Spain, the Balearics, Sardinia, central Europe, the Caucasus, Bulgaria, the Crimea, north Africa and Madagascar.

Genus ***CARINOPHYLLOCERAS*** Klinger, Wiedmann & Kennedy 1975

TYPE SPECIES. *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy 1975 : 658 ; pls 76–77 ; text-figs 1–3.

DIAGNOSIS. Phylloceratid ammonites with fastigate to distinctly keeled venters. Whorl section ovoid, higher than wide, with maximum width at umbilical margin ; narrowly umbilicated. Ornament typically phylloceratid, consisting of striae. Suture phylloid, with lituid I, trifid L, saddles E/L assymmetrically diphyllic, L/U_2 asymmetrically tetraphyllic. Saddles in U_3 asymmetrically diphyllic (Figs 8–9).

DISCUSSION. *Carinophylloceras* is unique amongst Cretaceous phylloceratids by virtue of the presence of a keel. Keeled phylloceratids occur in the Jurassic, e.g. *Harpophylloceras* Spath 1927 and *Meneghenicerias* Hyatt 1900. There are, however, no Cretaceous taxa referable to these genera and any affinity of *Carinophylloceras* with these forms may be ruled out.

The suture line of *Carinophylloceras* with an asymmetrical diphyllic saddle E/L and asymmetrical tetraphyllic L/U_2, the ornamentation, degree of evolution and to a lesser extent whorl section point to affinities with the Albian/Cenomanian *Phylloceras* (*Hypophylloceras*) *velledae* (sensu Wiedmann 1964), and to the Albian/Aptian *P.* (*H.*) *cypris cypris* Fallot & Termier (Wiedmann 1964 : fig. 50 ; pl. 13, fig. 3 etc.). Apart from the keel, the whorl section is somewhat intermediate between *P.* (*H.*) *velledae velledae* and *P.* (*H.*) *velledae morelianum*. The presence of a keel, however, clearly separates *Carinophylloceras collignoni* from the group of *P.* (*H.*) *velledae*. *Carinophylloceras* is a homeomorph of *Damesites*, and was originally believed to be a new species of that genus. The similarities are remarkable. Not only the whorl section and the presence and shape of the keel, but also the degree of shell involution,

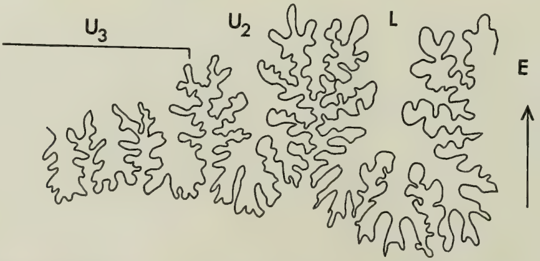


FIG. 8. External suture line of *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy. UPE B464, × 1·3.

the course of the ornamentation and even the external suture line show such similarities that these genera can scarcely be distinguished on their external morphology. Examination of the suture line, however, especially the internal part, reveals that it is typically phylloid with a lituid internal lobe (Fig. 9), a characteristic of all phylloceratinids (Wiedmann 1972 : 115). The internal lobe of *Damesites* as figured by Matsumoto (1954 : fig. 11) is intensively frilled and of desmoceratid type ; indeed *no* known desmoceratids possess a lituid internal lobe.

OCCURRENCE. Lower Albian (Albian III) of Zululand.

Carinophylloceras collignoni Klinger, Wiedmann & Kennedy

(Figs 8–9 ; Pl. 14 ; Pl. 15, figs 1–2)

1975 *Damesites* ? sp. nov. Kennedy & Klinger : 276.
1975 *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy : 658 ; pl. 76, figs 1a–b ; pl. 77, figs 1–3 ; text-figs 1–3.

HOLOTYPE. SAS A1577, from the Mzinene Formation, stream cliff section along the Mzinene River 1200 m NE of the farm Amatis, north of Hluhluwe, Zululand, South Africa, 27°58′03″ S, 32°18′34″ E. Loc. 35 of Kennedy & Klinger (1975).

MATERIAL. In addition to the holotype we have 39 paratypes : SAS UMS/2, SAS A1133 and BM(NH) C78639, C78644, C78647–8, C78767, C78769, C78770 from Loc. 35, and BM(NH) C78640–3, C78645–6, C78651 and C78768 from Loc. 36, both on the Mzinene River. SAS H93D/1, SAS H93/1, SAS H93/2, SAS 93/3, SAS H93/5, from Loc. 142, Nxala Estate, southern part of Mkuze Game Reserve, Zululand. SAS EM 91, SAS EM 92, SAS EM 77 from the Msunduzi Pan at 26°57′25″ S, 32°12′40″ E ; UPE B 33 from the same area, at 26°57′10″ S, 32°12′45″ E. SAS EM 245a, b, c, SAS EM 93, SAS EM 244, SAS EM 114, from the Ndumu region, northern Zululand at 26°55′55″ S, 32°12′55″ E. SAS LJE 134A, UPE B463, UPE B464, UPE B411 and BM(NH) C78649–50, from Loc. 174, and BM(NH) C78766 and C78771, from Loc. 171, both Mlambongwenya Spruit, northern Zululand. UPE B23, from Aloe Flats Estate, northern Zululand, at 26°59′50″ S, 32°11′50″ E.

All specimens are from the Mzinene Formation of late early Albian age (Albian III).

DIMENSIONS.		*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype	SAS A1577	149	60·5 (41)	88·5 (59)	0·68	8·5 (6)
Paratypes	SAS EM 244	123·5	44·5 (36)	68·0 (55)	0·65	8·0 (6·5)
	SAS H98/1	77·5	32·5 (41)	44·5 (58)	0·73	6·0 (8)
	SAS H93/3	108	40·5 (37)	63·5 (58)	0·64	7·5 (7)
	SAS UMS/2	132·5	47·0 (36)	77·5 (58)	0·60	9·0 (6·8)

DESCRIPTION. Coiling is moderately involute with a narrow funnel-shaped umbilicus (6–8% of diameter). Whorl section is subtrigonal with a fastigate to distinctly keeled venter. Maximum width is at the umbilical edge. In juvenile stages the venter is fastigate, but in the adult a distinct keel is developed. The

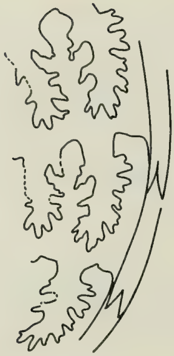


FIG. 9. Partial internal suture line of *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy, showing overlapping lituid internal lobe. SAS EM 114, × 8·3.

keel is of the floored type, and, depending on the mode of preservation, may be either present or absent on internal moulds.

Ornament consists of pronounced striae which arise at the umbilical wall, are bent forwards at first, then sweeping gently backwards near the middle of the flanks, being finally strongly projected on the outer part of the flanks. They are bundled at their origin, and much stronger on the outer part of the whorls and venter, producing a chevron-like ventrolateral and ventral ornament. On internal moulds the ornamentation is still present, though very much subdued.

Suture line as for genus. Auxiliary saddles in U_3 are triphyllic.

OCCURRENCE. Lower Albian (Albian III) of Zululand.

III. ACKNOWLEDGEMENTS

We are grateful to Dr H. W. Ball, Dr M. K. Howarth and Mr D. Phillips of the Department of Palaeontology, British Museum (Natural History), General M. Collignon (Moirans), Mr C. W. Wright (London), Professor Dr J. Wiedmann (Tübingen), Professor D. L. Visser (Pretoria), Dr C. K. Brain and Mrs E. Voigt (Transvaal Museum, Pretoria), Mr P. J. Rossouw (Pretoria), Mr M. R. Cooper (South African Museum, Cape Town) and the technical staff of the Department of Geology, Oxford, Geological Survey of South Africa, Pretoria, Institut für Geologie und Paläontologie, Tübingen, and Transvaal Museum, Pretoria, for their help and assistance in many ways. Thanks are also due to the Director, Geological Survey, Pretoria, for permission for one of us (H. C. K.) to publish these results.

IV. REFERENCES

ALMELA, A. & DE LA REVILA, J. 1957. Fósiles piritosos de Cretáceo de la Sierra de Ricote (Murcia). *Boln Inst. geol. min. Esp.*, Madrid, **68** : 45–83, pls 1–11.

ANDERSON, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap. geol. Soc. Am.*, New York, **16**, 244 pp., 84 pls.

ARNOULD-SAGET, S. 1951. Les ammonites pyriteuses du Tithonique supérieur et du Berriasien de Tunisie central. *Annls Mines Géol., Tunis*, **10** : 1–132, pls 1–11.

BARRABÉ, L. 1929. Contribution à l'étude stratigraphique et pétrographique du pays de Sakalave, Madagascar. *Mém. Soc. géol. Fr.*, Paris, n.s. **12** : 1–270, pls 1–10.

BESAIRIE, H. 1930. Recherches géologiques à Madagascar. Contribution à l'étude des ressources minérales. *Bull. Soc. Hist. nat. Toulouse*, **60** : 345–616 (1–272), pls 1–27.

—— 1936. Recherches géologiques à Madagascar. Première suite. La géologie du nord-ouest. *Mém. Acad. malgache*, Tananarive, **21** : 9–259, pls 1–24.

BEZNOSOV, N. V. 1958. *Jurassic ammonites of the northern Caucasus and Crimea. Phylloceratina and Lytoceratina.* 118 pp, 34 pls. Gostoptekhizdat, Leningrad. [In Russian.]

BOULE, M., LEMOINE, P. & THÉVENIN, A. 1906–07. Paléontologie de Madagascar. III – Céphalopodes crétacés des environs de Diego-Suarez. *Annls Paléont.*, Paris, **1** : 173–192, pls 14–20 (1906) ; **2** : 1–56, pls 1–8 (1907).

BREISTROFFER, M. 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Trav. Lab. Géol. Univ. Grenoble*, **26** : 1–88.

BUSNARDO, R. & DAVID, L. 1957. Contribution à l'étude des faunes d'Ammonoïdes de Medjez Sfa (Est Constantinois). *Publs Serv. Carte géol. Algér.*, Algiers, n.s. **13** : 67–123, pls 1–3.

COLLIGNON, M. 1928–29. Les Céphalopodes du Cénomanien pyriteux de Diego-Suarez. *Annls Paléont.*, Paris, **17** : 139–160 (1–24), pls 15–19 (1–5) (1928) ; **18** : 1–56 (25–79), pls 1–2 (6–7) (1929).

—— 1931. Faunes senoniennes du nord et de l'ouest de Madagacar. *Annls géol. Serv. Mines Madagascar*, Tananarive, **1** : 1–66, pls 1–9.

—— 1936. Fossiles du Turonien supérieur d'Antanitiloky. *In* BESAIRIE, H. Recherches géologiques à Madagascar. Première suite. La géologie du Nord-Ouest. *Mém. Acad. malgache*, Tananarive, **21** : 200–202, pl. 21.

—— 1937. Les ammonites pyriteuses de l'Aptien d'Antanatanamirafy. *Annls Paléont.*, Paris, **26** : 107–132, pls 16–18.

—— 1938. Ammonites Campaniennes et Maastrichtiennes de l'ouest et du sud de Madagascar. *Annls géol. Serv. Mines Madagascar*, Tananarive, **9** : 55–118, pls 1–9.

—— 1949a. Faune néocomienne des couches à *Crioceras* de Belohasifaka (cercle de Sitampiky). *Annls géol. Serv. Mines Madagascar*, Tananarive, **15** : 53–83, pls 8–13.

—— 1949b. La faune albiene d'Ambarimaninga. *Annls géol. Serv. Mines Madagascar*, Tananarive, **16** : 1–128, pls 1–22.

—— 1950. L'Albien de Mokaraha. *Annls géol. Serv. Mines Madagascar*, Tananarive, **17** : 57–85, pls 10–14.

—— 1956. Ammonites néocrétacées du Menabe (Madagascar). IV. – Les Phylloceratidae. V. – Les Gaudryceratidae. VI. – Les Tetragonitidae. *Annls géol. Serv. Mines Madagascar*, Tananarive, **23** : 1–106, pls 1–11.

—— 1962. *Atlas des fossiles caractéristiques de Madagascar* (*Ammonites*). **VIII** (*Berriasien, Valanginien, Hauterivien, Barremien*) : 96 pp, pls 176–214. Service Géologique, Tananarive.

—— 1963. *Atlas des fossiles caractéristiques de Madagascar* (*Ammonites*). **X** (*Albien*) : xv+184 pp, pls 241–317. Service Géologique, Tananarive.

—— 1964. *Atlas des fossiles caractéristiques de Madagascar* (*Ammonites*). **XI** (*Cénomanien*) : xi+152 pp, pls 318–375. Service Géologique, Tananarive.

—— 1966. *Atlas des fossiles caractéristiques de Madagascar* (*Ammonites*). **XIV** (*Santonien*) : x+134 pp, pls 455–513. Service Géologique, Tananarive.

COQUAND, H. 1880. Études supplémentaires sur la paléontologie algérienne. *Bull. Acad. Hippone*, Bône, **15** : 1–449.

CRICK, G. C. 1907a. The Cephalopoda from the deposit at the North End of False Bay, Zululand. *Rep. geol. Surv. Natal Zululand*, Pietermaritzburg, **3** : 163–234, pls 10–15.

—— 1907b. The Cephalopoda from the tributaries of the Manuan Creek, Zululand. *Rep. geol. Surv. Natal Zululand*, Pietermaritzburg, **3** : 235–249.

DRUSHCHITZA, V. V. & KUDRYAVTSEVA, M. P. 1960. *Atlas of Lower Cretaceous fauna of the northern Caucasus and Crimea.* 396 pp, 149 pls. Gostoptekhizdat, Moscow. [In Russian.]

FABRE, S. 1940. Le crétacé supérieur de la Basse-Provence occidentale, 1. Cénomanien et Turonien. *Annls Fac. Sci. Marseille,* Sér. II, **14** : 355 pp, 10 pls.

FALLOT, P. & TERMIER, H. 1923. Ammonites nouvelles des Îles Baléares. *Trab. Mus. nac. Cienc. nat. Madr.*, ser. Geol. **32** : 1–83, pls 1–6.

FORBES, E. 1846. Report on the Cretaceous fossil invertebrates from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Trans. geol. Soc. Lond.*, (2) **7** : 97–174, pls 7–19.

GABB, W. M. & MEEK, F. B. 1864. *Palaeontology of California,* **1** : xx+243 pp, 32 pls. Geol. Surv. Calif., San Francisco.

HENDERSON, R. A. 1970. Ammonoidea from the Mata Series (Santonian–Maastrichtian) of New Zealand. *Spec. Pap. Palaeont.*, London, **6** : 81 pp, 15 pls.

JONES, D. L. 1963. Upper Cretaceous (Campanian and Maastrichtian) ammonites from southern Alaska. *Prof. Pap. U.S. geol. Surv.*, Washington, **432** : 1–53, pls 1–41.

KARAKASH, N. I. 1907. Le Crétacé de la Crimeé et sa faune. *Trudy̆ imp. S.-Peterb. Obshch. Estest.*, **32** : 1–482, pls 1–28.

KENNEDY, W. J. & KLINGER, H. C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **25** (4) : 263–315, plate.

KLINGER, H. C., WIEDMANN, J. & KENNEDY, W. J. 1975. A new carinate phylloceratid ammonite from the early Albian (Cretaceous) of Zululand, South Africa. *Palaeontology,* London, **18** (3) : 657–664, pls 76–77.

KOSSMAT, F. 1895–98. Untersuchungen über die sudindische Kreideformation. *Beitr. Paläont. Geol. Öst-Ung.*, Vienna and Leipzig, **9** (1895) : 97–203 (1–107), pls 15–25 (1–11) ; **11** (1897) : 1–46 (108–153), pls 1–8 (12–19) ; **12** (1898) : 89–152 (154–217), pls 14–19 (20–25).

McLEARN, D. 1972. Ammonoids of the Lower Cretaceous sandstone member of the Haida Formation, Skidegate Inlet, Queen Charlotte Islands, western British Columbia. *Bull. geol. Surv. Can.*, Ottawa, **188** : 1–78, 45 pls.

MAHMOUD, I. G. EL-DIN 1955. Études paléontologiques sur la faune crétacique du massif du Moghara (Sinaï, Égypte). *Publs Inst. Désert Égypte,* Heliopolis, **8** : 1–192, 19 pls.

MARSHALL, P. 1926. The upper Cretaceous ammonites of New Zealand. *Trans. Proc. N.Z. Inst.*, Wellington, **56** : 129–210, pls 19–47.

MATSUMOTO, T. 1943. A short note on the Japanese Cretaceous Phylloceratidae. *Proc. imp. Acad. Japan,* Tokyo, **18** (for 1942) : 674–676.

—— 1953. The ontogeny of *Metaplacenticeras subtilistriatum* (Jimbo). *Jap. J. Geol. Geogr.*, Tokyo, **23** : 139–150, pl. 13.

—— 1954. Appendix. Selected Cretaceous leading ammonites in Hokkaido and Saghalien. *In* MATSUMOTO, T. (Ed.) *The Cretaceous System in the Japanese Islands* : 243–313, pls 17–36. Jap. Soc. Promotion Sci., Tokyo.

—— 1959. Cretaceous ammonites from the Upper Chitina Valley, Alaska. *Mem. Fac. Sci. Kyushu Univ.* (D), **8** : 49–90, pls 12–29.

MICHELIN, H. 1834. *Ammonites velledae. Magasin Zool.*, Paris, **3** : C IV, pl. 35.

NEUMAYR, M. 1885. Die geographische Verbreitung der Juraformation. *Denkschr. Akad. Wiss. Wien,* **50** : 57–142, pl. 1.

OPPEL, A. 1865. Die Tithonische Étage. *Z. dt. geol. Ges.*, Berlin, **17** : 535–558.

ORBIGNY, A. D'. 1840–42. *Paléontologie française. Terrains Crétacés I. Céphalopodes.* 662 pp, 148 pls. Paris.

—— 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés,* **2**. 427 pp. Paris.

PARONA, C. F. & BONARELLI, G. 1897. Fossili albani d'Escragnolles, del Nizzardo e della Liguria occidentale. *Palaeontogr. ital.*, Pisa, **2** : 53–112, pls 10–14.

PERVINQUIÈRE, L. 1907. *Carte géologique de la Tunisie. Études de paléontologie tunisienne,* 1. *Céphalopodes des terrains secondaires.* 438 pp, 27 pls. Paris.

—— 1910. Sur quelques ammonites du Crétacé algérien. *Mém. Soc. géol. Fr. Paléont.*, Paris, **42** : 1–86, 7 pls.

RAWSON, P. F. 1966. A phylloceratid ammonite from the Speeton Clay (Lower Cretaceous) of Yorkshire. *Palaeontology*, London, **9** : 455–457, pl. 72.

ROUSSEAU, L. 1842. Description des principaux fossiles de la Crimée. *In* DÉMIDOFF, A. DE 1840–42. *Voyage dans la Russie méridionale et la Crimée par la Hongrie, la Valachie et la Moldavie* (&c.) **2** : 781–823, Atlas pls 1–12. Paris.

SAYN, G. 1891. Description des ammonites nouvelles ou peu connues du Crétacé inférieur du sud-est de la France. *Mem. Soc. géol. Fr.*, Paris, **17** : 679–688, pl. 17.

—— 1901–07. Les ammonites pyriteuses des marnes valanginiennes du sud-est de la France. *Mém. Soc. géol. Fr.*, Paris, **23** : 1–66, pls 1–6.

—— 1920. Les *Phylloceras* gargasiens du sud-est de la France (espèces nouvelles ou peu connues). *In* KILIAN, W. Contribution à l'étude des céphalopodes paléocrétacés du sud-est de la France. *Mém. Serv. Carte géol. dét. France*, Paris : 191–203, pl. 1.

SHIMIZU, S. 1935. The Upper Cretaceous cephalopods of Japan, Part I. *J. Shanghai Sci. Inst.*, sect. 2, **1** : 159–226.

SIMONOVICH, S., BATSEVICH, L. & SOROKIN, A. 1877. Description of the geology of the Kutais region etc. *Mater. Geol. Kavk.*, Tiflis, **1876** : 1–112, pls 1–8.

SPATH, L. F. 1921a. On Cretaceous Cephalopoda from Zululand. *Ann. S. Afr. Mus.*, Cape Town, **12** : 217–321, pls 19–26.

—— 1921b. On Upper Cretaceous Ammonoidea from Pondoland. *Ann. Durban Mus.*, **3** : 39–57, pls 6, 7.

—— 1922. On the Senonian ammonite fauna of Pondoland. *Trans. R. Soc. S. Afr.*, Cape Town, **10** : 113–147, pls 5–9.

—— 1923–43. A monograph of the Ammonoidea of the Gault. *Palaeontogr. Soc.* (Monogr.), London, 787 pp, 72 pls.

—— 1925. On Upper Albian Ammonoidea from Portuguese East Africa, with an appendix on Upper Cretaceous ammonites from Maputoland. *Ann. Transv. Mus.*, Pretoria, **11** : 179–200, pls 28–37.

—— 1927. Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). *Mem. geol. Surv. India Palaeont. indica*, Calcutta, n.s. **11** : 1–71, pls 1–7.

STOLICZKA, F. 1863–66. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India Palaeont. indica*, Calcutta (3) **1** : 41–56, pls 26–31 (1863) ; **2–5** : 57–106, pls 32–54 (1864) ; **6–9** : 107–154, pls 55–80 (1865) ; **10–13** : 155–216, pls 81–94 (1866).

TATE, R. 1865. Correlation of the Cretaceous Formations of the north-east of Ireland. *Q. Jl geol. Soc. Lond.*, **21** : 15–44, pls 3–6.

TOUCAS, A. 1890. Étude de la faune des couches Tithonique de l'Ardèche. *Bull. Soc. géol. Fr.*, Paris, **18** : 560–630, pls 13–18.

USHER, J. L. 1952. Ammonite faunas of the Upper Cretaceous of Vancouver Island, British Columbia. *Bull. geol. Surv. Can.*, Ottawa, **21** : 1–182, pls 1–30.

VAN HOEPEN, E. C. N. 1920. Description of some Cretaceous ammonites from Pondoland. *Ann. Transv. Mus.*, Pretoria, **7** : 142–147, pls 24–26.

—— 1921. Cretaceous Cephalopoda from Pondoland. *Ibid.*, **8** : 1–48, pls 1–11.

VENZO, S. 1936. Cefalopodi del Cretacea medio-superiore dello Zululand. *Palaeontogr. ital.*, Pisa, **36** : 59–133, pls 5–12.

WIEDMANN, J. 1962a. Die systematische Stellung von *Hypophylloceras* Salfeld. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **115** : 243–256, pl. 16.

—— 1962b. Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1. Phylloceratina, Lytoceratina. *Palaeontographica*, Stuttgart, A **118** : 119–237, pls 8–14.

—— 1964. Unterkreide-Ammoniten von Mallorca, 2. Lieferung : Phylloceratina. *Abh. math.-naturw. Kl. Akad. Wiss. Mainz*, Jahr. **1963** (4) : 157–264, pls 11–21.

—— 1972. Neue Vorstellungen über Stammesgeschichte und System der Kreideammoniten. *Proc. int. palaeont. Un., int. geol. Congr. XXIII Sess., Czechoslovakia 1968* : 93–120, 1 pl. Warsaw.

WIEDMANN, J. & DIENI, I. 1968. Die Kreide Sardiniens und ihre Cephalopoden. *Palaeontogr. ital.*, Pisa, **64** : 1–171, 18 pls.

WOODS, H. 1906. The Cretaceous fauna of Pondoland. *Ann. S. Afr. Mus.*, Cape Town, **4** : 275–350, pls 33–44.

YOKOYAMA, M. 1890. Versteinerungen aus der japanischen Kreide. *Palaeontographica*, Stuttgart, **36** : 159–202, pls 18–25.

ZITTEL, K. A. 1868. Die Cephalopoden der Stramberger Schichten. *In* OPPEL, A. *Palaeont. Mitth. Mus. k. Bayer. St.* **2** (1) : 1–118, pls 1–24. Stuttgart.

ZWIERZYCKI, J. 1914. Die Cephalopodenfauna der Tendaguru-Schichten in Deutsch-Ostafrika. *Arch. Biontol.*, Berlin, **3** (4) : 7–96, pls 1–10.

V. INDEX

The page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

acknowledgements 374
Ammonites baborensis 371
  cylindricus 352
  partschi 369
  ramosus 359
  rouyanus 371
  serus 352
  subalpinus 355
  velledae 355, 360, 364
  zetes 352
Aphroditiceras 354 ; see *Salfeldiella*

Calaiceras 369
Carinophylloceras **372–3**
  collignoni 350, 372, 372*, **373–4**, 374* ; pls 14–15

Damesites 372–3
  ? sp. nov. 373
dimensions of specimens 351

Epiphylloceras 351, 354, 363, 369, 371
  mikobokense 368
  radiatum 369
erratum 380
Euphylloceras 354
  serum 352
  velledae 360

field localities 351

Geyeroceras see *Phylloceras*
Goretophylloceras 354

Hantkeniceras 351
Harpophylloceras 372
Heterophylloceras 351
Hoplophylloceras 369
Hypophylloceras 369 &c. ; see *Phylloceras*
  aphrodite 358
  cottreaui 369
  seresitense 364
  surya 369
Hyporbulites 354, 363
  androiavense 365
  betieri 352, 354
  hoepeni 366–8, 368*
  seresitensis 364
    renaudiensis 364
  woodsi 366

location of specimens 350

Macrophylloceras 369
Meneghenіceras 372

Neophylloceras 351, 354, 363
  hetonaiense 368
  lambertense 368
  marshalli 368
  nera 368
  seresitense 364

Paraphylloceras 354
Partschiceras **369**
  baborense 371–2
  sp. juv. cf. *baborense* 350, **371–2** ; pl. 6, figs 2–3
  besairiei besairiei 370
    tsianalokensis 370
  bistriatum 370

  ezoense 370
  forbesianum 370–1
  inflatum 370
  ? *japonicum* 356, 358
  marshalli 370
  minimum 370
  occlusum 370
  umzambiense 350, **370–1**, 371* ; pl. 13, fig. 2
  whiteavesi 370
  zelandicum 370
Partschiphylloceras 369
Phylloceras **351** ; see also *Hyporbulites*
  androiavensis 365
  aphrodite 355, 358
  ellipticum 355–6, 358
  escragnollensis 358
  aff. *grothi* 358
  heterophyllum 351
  improvisum 356
  japonicum 356
  nera 366, 368 ; pl. 13, fig. 3
  onoense 352, 354
  cf. *perlobatum* 352
  ex aff. *ramosi* 364
  robionense 352–4
  sablyense 354
  semistriatum 352
  seresitense tanit 364–5
  serum 352, 354
    perlobata 352–3
  spathi 352–3
  aff. *surya* 368
  thetys 352, 354, 359
  umzambiense 370
  velledae 360–1, 364–5
    inflatum 362
    seresitense 364
  woodsi 366
  sp. 360–1, 366
  (*Geyeroceras*) 352
    cylindricus 352
  (*Hypophylloceras*) 352, **354–69**
    algeriense 366
    androiavense 350, **365–6** ; pl. 4, fig. 7
    aphrodite 350, 355, **358–9** ; pl. 3, fig. 3
    aptiense applanatum 355, 358–9
      aptiense 355, 358–9
    aff. *californicum* 363
    cypris cypris 359, 362, 366, 372
      cytherae 359, 362, 366
    fortunei 355, 358
    hoepeni 368
    infundibuliformis 368
    improvisum 355–6, 358
    mikobokense 350, **368–9** ; pl. 12, fig. 1
    moreti 355, 358
    nera 368
    onoense 352, 359
    pervinquierei 360
    ponticuli 359
    sablyense 355
    sardoum 355, 358
    seresitense 354, 359, 362, **363**, 365 ; pl. 4, fig. 6
      boulei 363, 365
      seresitense 350, 363, **364–5** ; pl. 6, fig. 4 ; pl. 7, fig. 4 ; pl. 9
      tanit 363, 365
    subalpinum ellipticum 350, 354, **355–8**, 356*, 357*, 368 ; pl. 4, figs 1–4 ; pl. 5, figs 2–3 ; pl. 12, fig. 2
      subalpinum 354, 357–8, 368
    subseresitense 355, 358
    thetys diegoi 355, 358
      majoricense 355, 358
      thetys 354–5, 358–9
    velledae 354, 359, **360**, 362, 372 ; pl. 6, fig. 1
      aschiltaense 359–60, 362
      inflatum 350, 359–60, **362–3** ; pl. 13, fig. 1
      morelianum 359–60, 362, 372
      velledae 350, 359, **360–2**, 363, 372 ; pl. 4, fig. 5 ; pl. 5, fig. 4 ; pl. 7, figs 2–3 ; pls 8, 10, 11
    sp. aff. *velledae* 350, **363** ; pl. 5, fig. 1 ; pl. 7, fig. 1
    woodsi 367–8
      infundibuliformis 368
      woodsi 350, **366–8**, 366*, 367*, 368* ; pl. 13, figs 3–5
  (*Phylloceras*) 351, **352–4**
    heterophyllum 352
    serum 350, **352–4**, 353* ; pls 1–2 ; pl. 3, figs 1–2
    spathi 352, 354
  (*Salfeldiella*) *guettardi* 358
  (*Zetoceras*) 352
    zetes 352

Phylloceratacae 351–74
Phylloceratidae 351–74
Phylloceratinae 351–74
Phyllopachyceras 369
  umzambiense 370
Procliviceras 369
Pseudophylloceras 351

Rhacoceras 351

Salfeldiella (*Aphroditiceras*) see *Phylloceras aphrodite venus* 358

Texanites oliveti Zone 368, 371

Xeniophylloceras 351

Zetoceras see *Phylloceras*

VI. ERRATUM

The following error has been noted in the first paper of this series (*Bull. Br. Mus. nat. Hist.* (Geol.), **25** (4) : 263–315) :

For 'Besaire' *read* 'Besairie' *throughout.*

W. J. KENNEDY
Dept of Geology & Mineralogy
UNIVERSITY OF OXFORD
PARKS ROAD
OXFORD OX1 3PR
ENGLAND

H. C. KLINGER
SOUTH AFRICAN MUSEUM
P.O. BOX 61
CAPE TOWN 8000
REPUBLIC OF SOUTH AFRICA

Accepted for publication 12 February 1976

PLATE 1

Phylloceras (Phylloceras) serum (Oppel)
BM(NH) C78658, Makatini Formation, Barremian I, Loc. 170, Mlambongwenya Spruit, northern Zululand. × 1. (p. 352 ; see also Pl. 2 and Pl. 3, figs 1–2.)

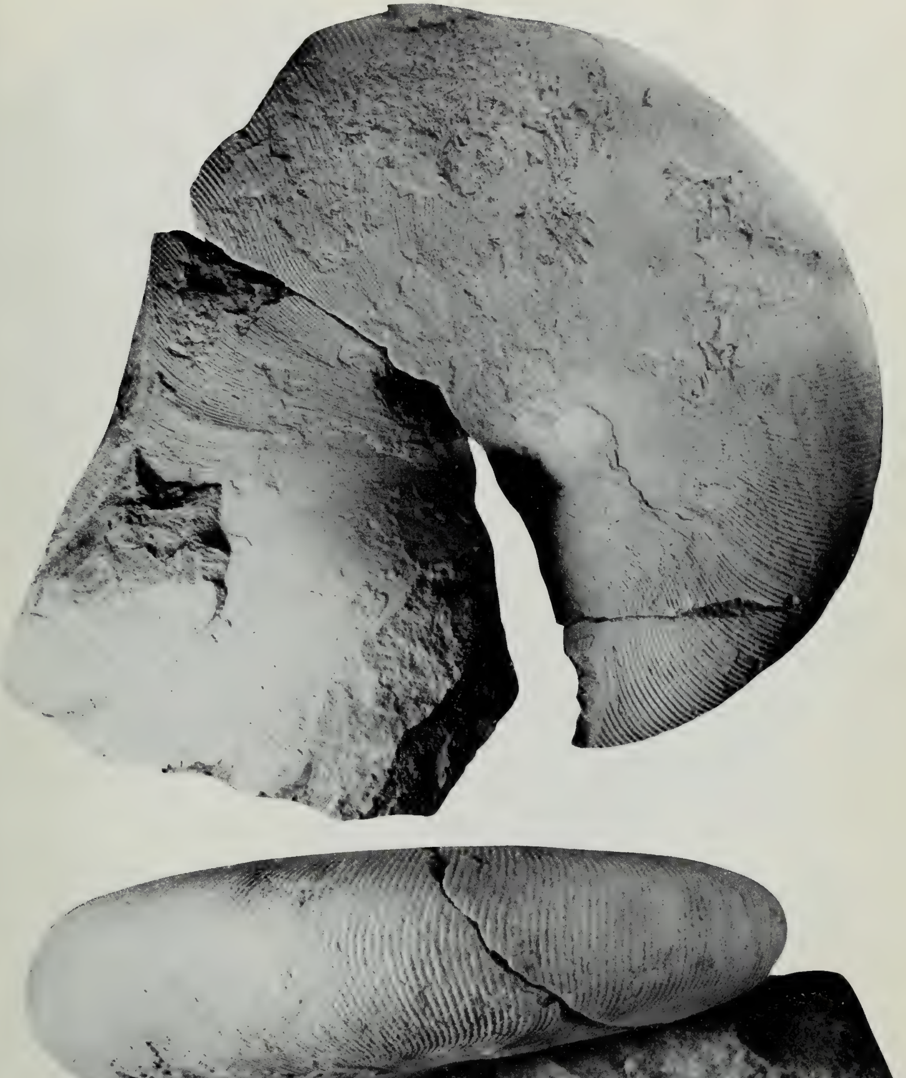
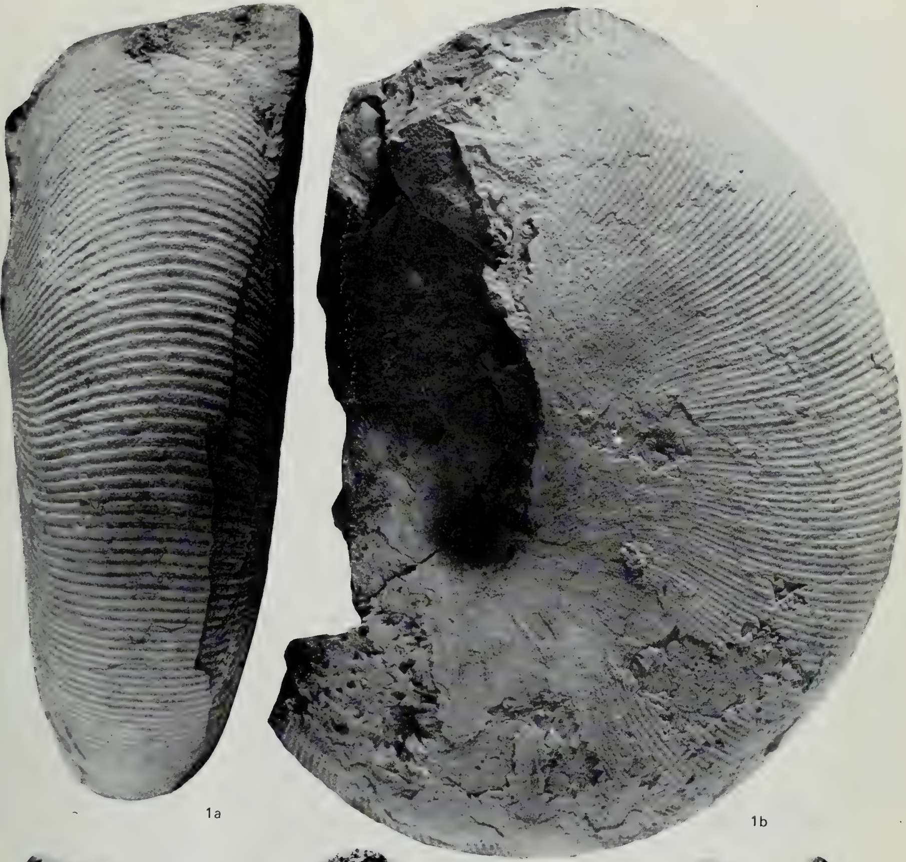


PLATE 2

Phylloceras (Phylloceras) serum (Oppel)

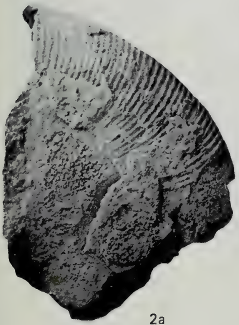
Makatini Formation, Barremian I, Loc. 170, Mlambongwenya Spruit, northern Zululand.
(p. 352 ; see also Pl. 1 and Pl. 3, figs 1–2.)

FIG. 1a, b. BM(NH) C78660, × 1.
FIG. 2a–g. BM(NH) C78659. a–d, × 1. e–g, × 2.

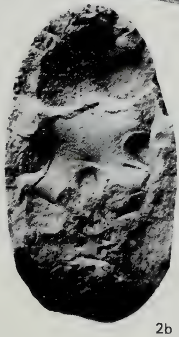


1a

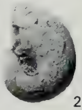
1b



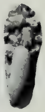
2a



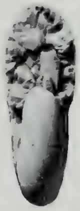
2b



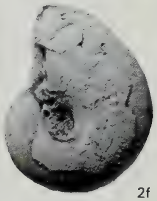
2c



2d



2e



2f

2g

PLATE 3

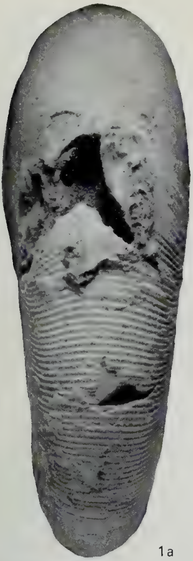
Phylloceras (Phylloceras) serum (Oppel)

Makatini Formation, Barremian I, Loc. 170, Mlambongwenya Spruit, northern Zululand. × 1. (p. 352 ; see also Pls 1–2.)

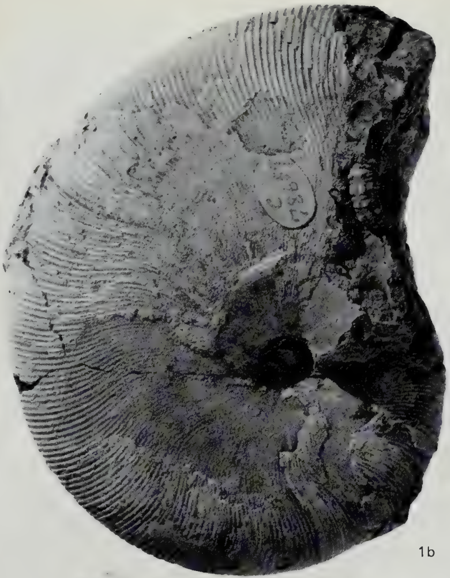
Fig. 1a–c. BM(NH) C78657.
Fig. 2a–b. BM(NH) C78661.

Phylloceras (Hypophylloceras) aphrodite Fallot & Termier

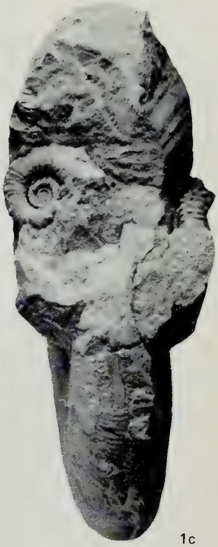
Fig. 3. BM(NH) C78691, Mzinene Formation, Albian V, Loc. 51 (Bed 1), Mzinene River, Zululand. × 1. (p. 358.)



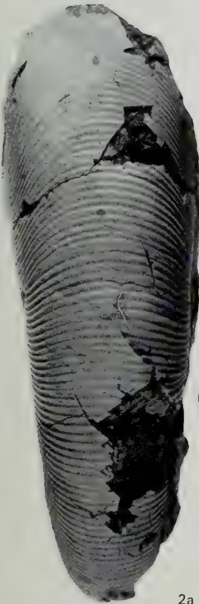
1a



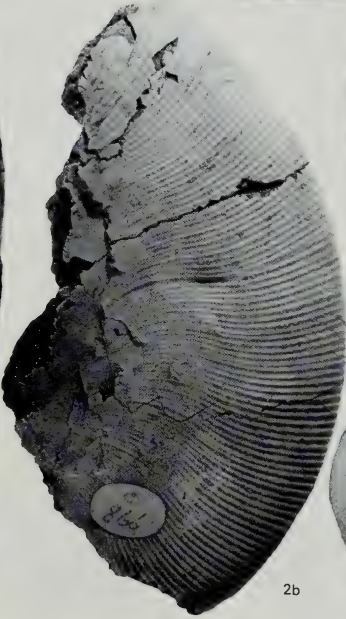
1b



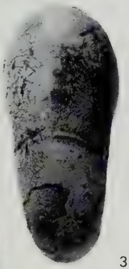
1c



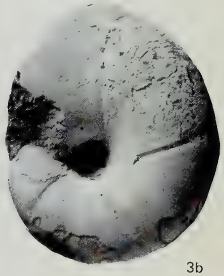
2a



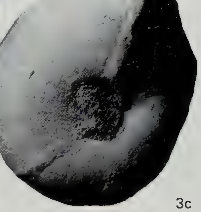
2b



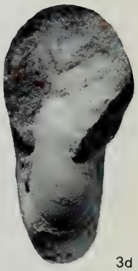
3a



3b



3c



3d

PLATE 4

Phylloceras (Hypophylloceras) subalpinum ellipticum Kossmat
(p. 355 ; see also Pl. 5, figs 2–3 and Pl. 12, fig. 2.) All × 1.

FIG. 1. BM(NH) C78665, Mzinene Formation, Albian V, Loc. 66, Munywana Creek Zululand.

FIG. 2. BM(NH) C78664, Mzinene Formation, Albian V, Loc. 54, Munywana Creek, Zululand.

FIG. 3. BM(NH) C18139, figured Crick (1907a : pl. 10, figs 12, 12a), Mzinene Formation, Skoenberg region on the Lower Mzinene River, Zululand, probably Cenomanian III.

FIG. 4. SAS A116, Mzinene Formation, Albian V, Loc. 67, Munywana Creek, Zululand.

Phylloceras (Hypophylloceras) velledae velledae (Michelin)

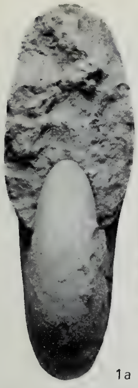
FIG. 5. BM(NH) C78683, Mzinene Formation, Albian V, Loc. 51 (Bed 6), Mzinene River, Zululand. × 1. (p. 360 ; see also Pl. 5, fig. 4 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 and Pls 8, 10, 11.)

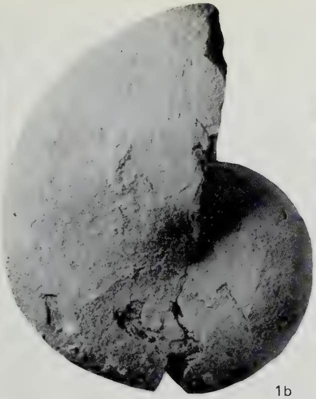
Phylloceras (Hypophylloceras) seresitense Pervinquière

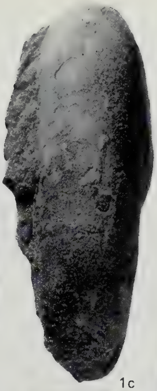
FIG. 6. BM(NH) C18138, figured Crick (1907a : pl. 10, figs 10–10a), Mzinene Formation, Cenomanian, Skoenberg region, Mzinene River, Zululand. × 1. (p. 364 ; see also Pl. 6, fig. 4 ; Pl. 7, fig. 4 and Pl. 9.)

Phylloceras (Hypophylloceras) androiavense Besairie

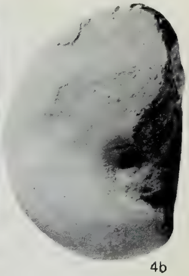
FIG. 7. BM(NH) C78667, Mzinene Formation, Albian V, Loc. 54, Mzinene River, Zululand. × 1. (p. 365.)

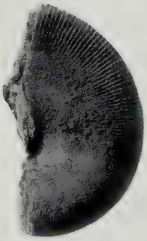

1a

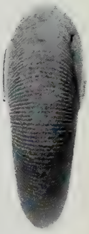

1b

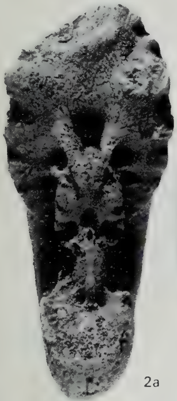

1c

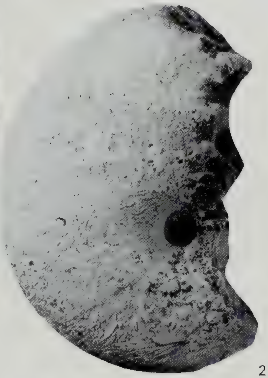
4a

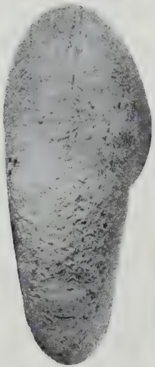

4b

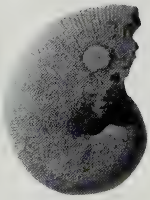

5a

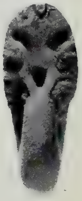

5b

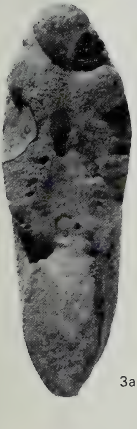

2a

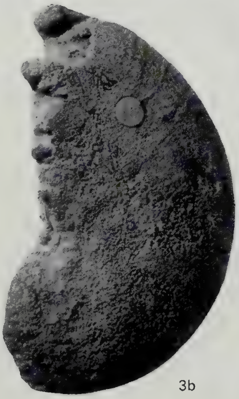

2b

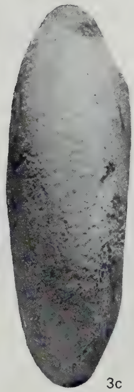

2c

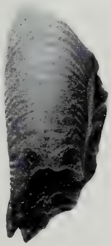

6a


6b


3a


3b


3c


7a

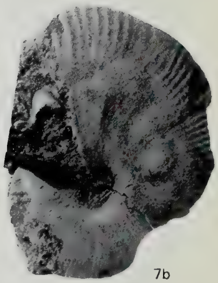

7b

PLATE 5

Phylloceras (Hypophylloceras) sp. aff. ***velledae*** (Michelin)

Fig. 1. BM(NH) C78696, Mzinene Formation, Albian V, Loc. 51, Mzinene River, Zululand (found loose). × 1. (p. 363 ; see also Pl. 7, fig. 1.)

Phylloceras (Hypophylloceras) subalpinum ellipticum Kossmat

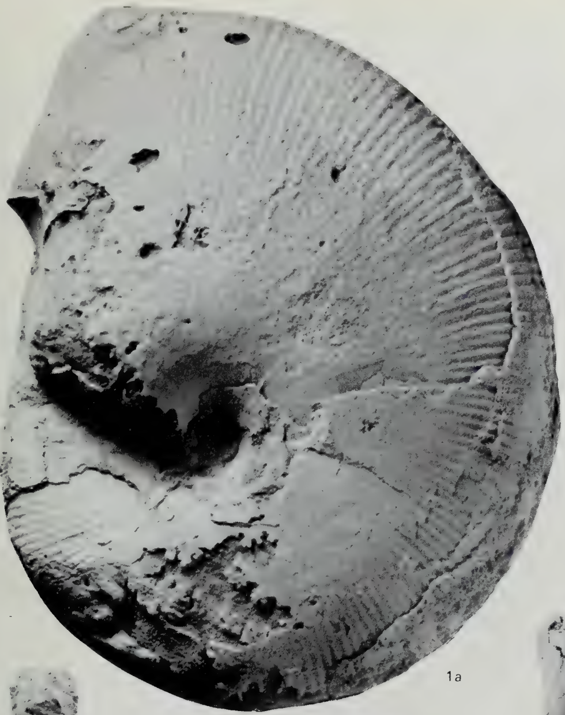
(p. 355 ; see also Pl. 4, figs 1–4 and Pl. 12, fig. 2.) All × 1·25.

Fig. 2. BM(NH) C78663, Mzinene Formation, Albian V, Loc. 64 (Bed 4), Munywana Creek, Zululand.

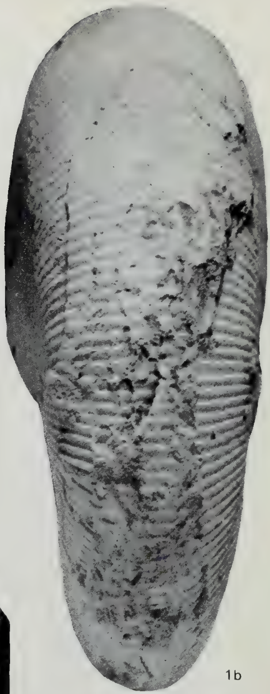
Fig. 3. BM(NH) C78662, Mzinene Formation, Albian V, Loc. 51 (Bed 6), Mzinene River, Zululand.

Phylloceras (Hypophylloceras) velledae velledae (Michelin)

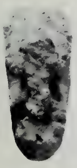
Fig. 4. BM(NH) C78672, Mzinene Formation, Albian V, Loc. 56, Mzinene River, Zululand. × 1. (p. 360 ; see also Pl. 4, fig. 5 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 and Pls 8, 10, 11.)



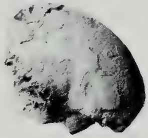
1a



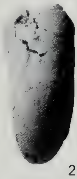
1b



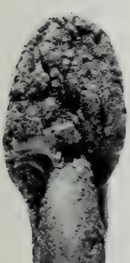
2a



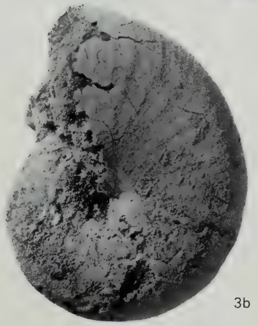
2b



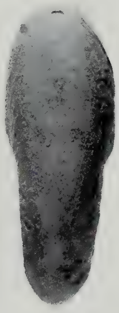
2c



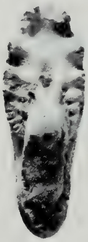
3a



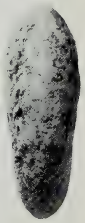
3b



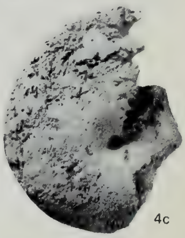
3c



4a



4b



4c

PLATE 6

Phylloceras (Hypophylloceras) velledae (Michelin)

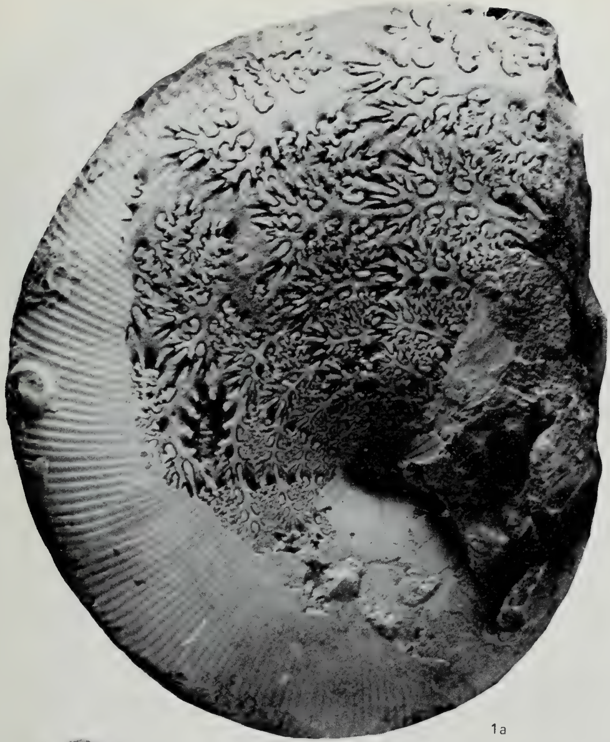
FIG. 1. SAS Z19a, from Haughton's (1936 : 291, fig. 3) Loc. 19. × 1. (p. 360 ; typical form see also Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 7, figs 2–3 and Pls 8, 10, 11.)

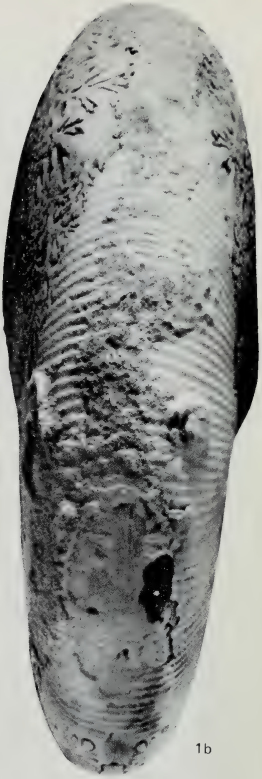
Partschiceras sp. juv. ? cf. **_baborense_** (Coquand)

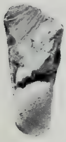
FIGS 2–3. BM(NH) C78693, Makatini Formation, Barremian I, Loc. 170, Mlambongwenya Spruit, northern Zululand. × 1 ; 3a–3b × 2. (p. 371.)

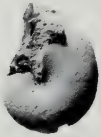
Phylloceras (Hypophylloceras) seresitense seresitense Pervinquière

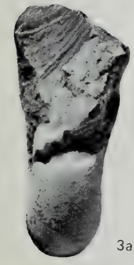
FIG. 4. BM(NH) C18137, figured Crick (1907a : pl. 10, figs 11–11a), Mzinene Formation, Cenomanian, Skoenberg Region, Mzinene River, Zululand. × 1. (p. 364 ; see also Pl. 4, fig. 6 ; Pl. 7, fig. 4 and Pl. 9.)

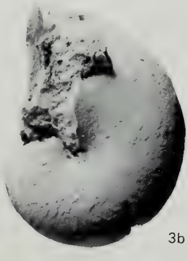

1a

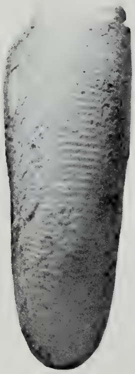

1b


2a


2b


3a


3b


4a

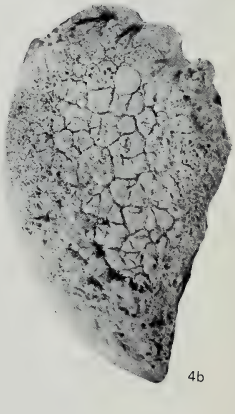

4b

PLATE 7

Phylloceras (Hypophylloceras) sp. aff. **velledae** (Michelin)

FIG. 1. BM(NH) C78695, Mzinene Formation, Albian V, Loc. 56, Mzinene River, Zululand. × 1. (p. 363 ; see also Pl. 5, fig. 1.)

Phylloceras (Hypophylloceras) velledae velledae (Michelin)

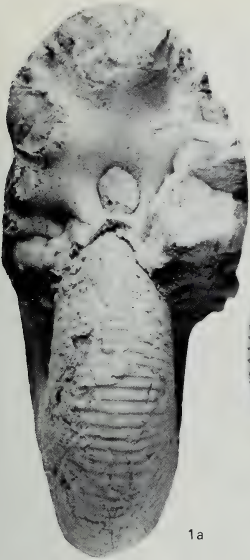
(p. 360; see also Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 6, fig. 1 and Pls 8, 10, 11.) Both × 1.

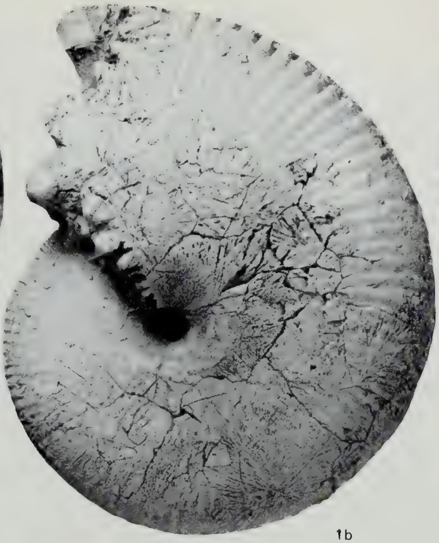
FIG. 2. BM(NH) C78673, Mzinene Formation, Albian V, Loc. 56, Mzinene River, Zululand.

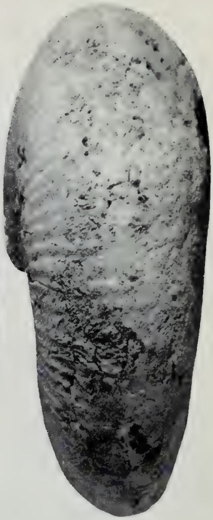
FIG. 3. BM(NH) C78684, Mzinene Formation, Albian V, Loc. 51 (Bed 12 or 13), Mzinene River, Zululand.

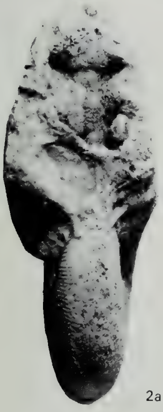
Phylloceras (Hypophylloceras) seresitense seresitense Pervinquière

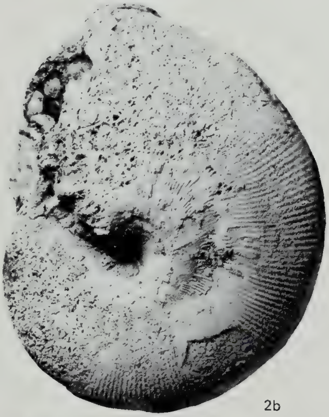
FIG. 4. BM(NH) C78690, Mzinene Formation, ? Cenomanian III, The Skoenberg, Mzinene River, Zululand. × 1. (p. 364 ; see also Pl. 4, fig. 6 ; Pl. 6, fig. 4 and Pl. 9.)

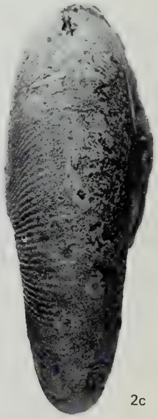

1a

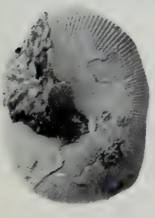

1b

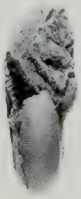

1c

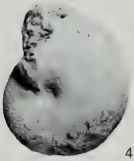

2a


2b


2c


3a


3b


4a

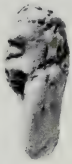

4b

PLATE 8

Phylloceras (Hypophylloceras) velledae velledae Michelin
BM(NH) C78668, Mzinene Formation, Albian IV, Loc. 51 (Bed 1), Mzinene River, Zululand. ×0·9 ; actual diameter 208 mm. (p. 360 ; see also Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 and Pls 10–11.)

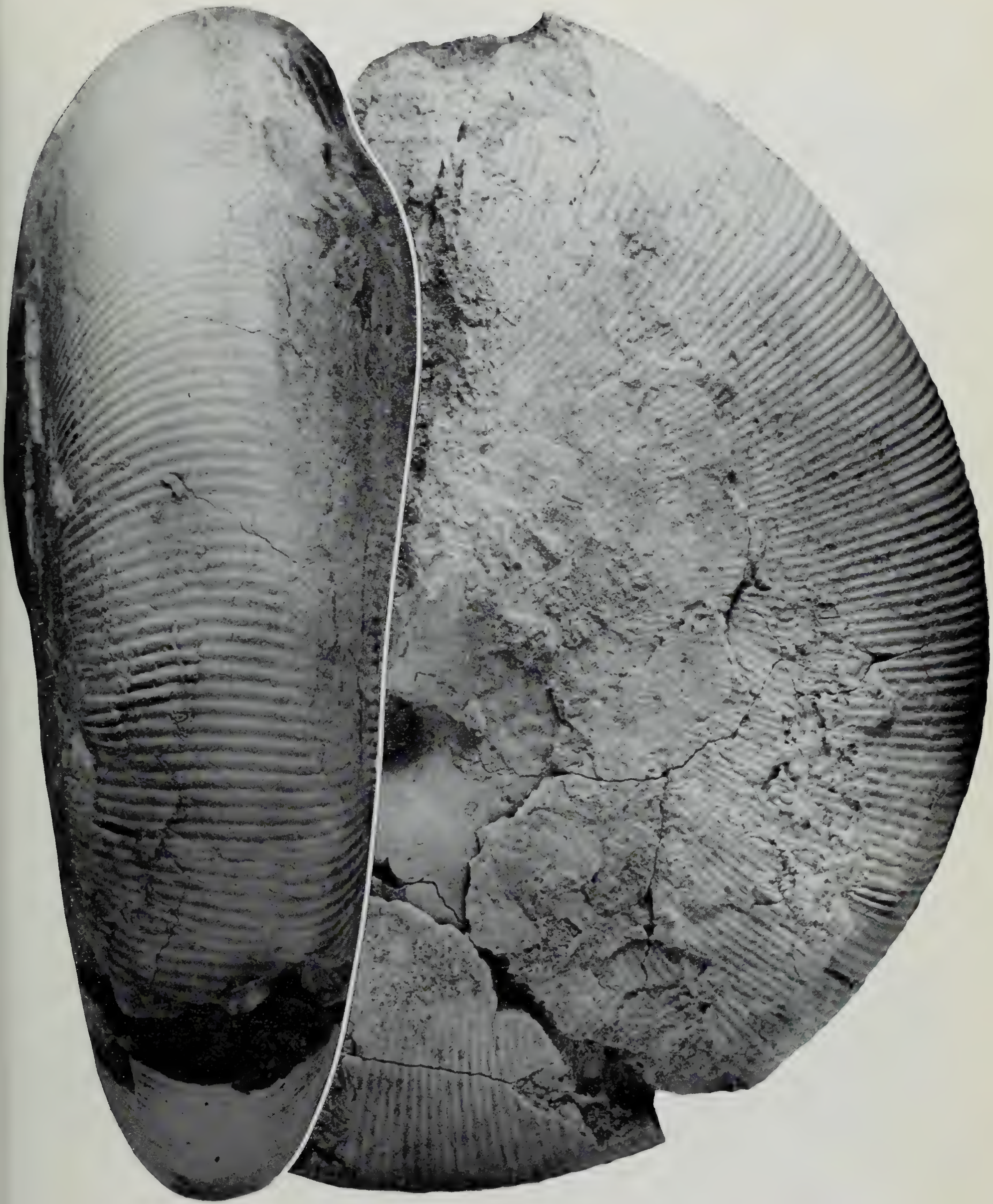


PLATE 9

Phylloceras (Hypophylloceras) seresitense seresitense Pervinquière
SAS A1401, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand.
× 0·74 ; actual diameter 190 mm. (p. 364 ; see also Pl. 4, fig. 6 ; Pl. 6, fig. 4 and Pl. 7, fig. 4.)

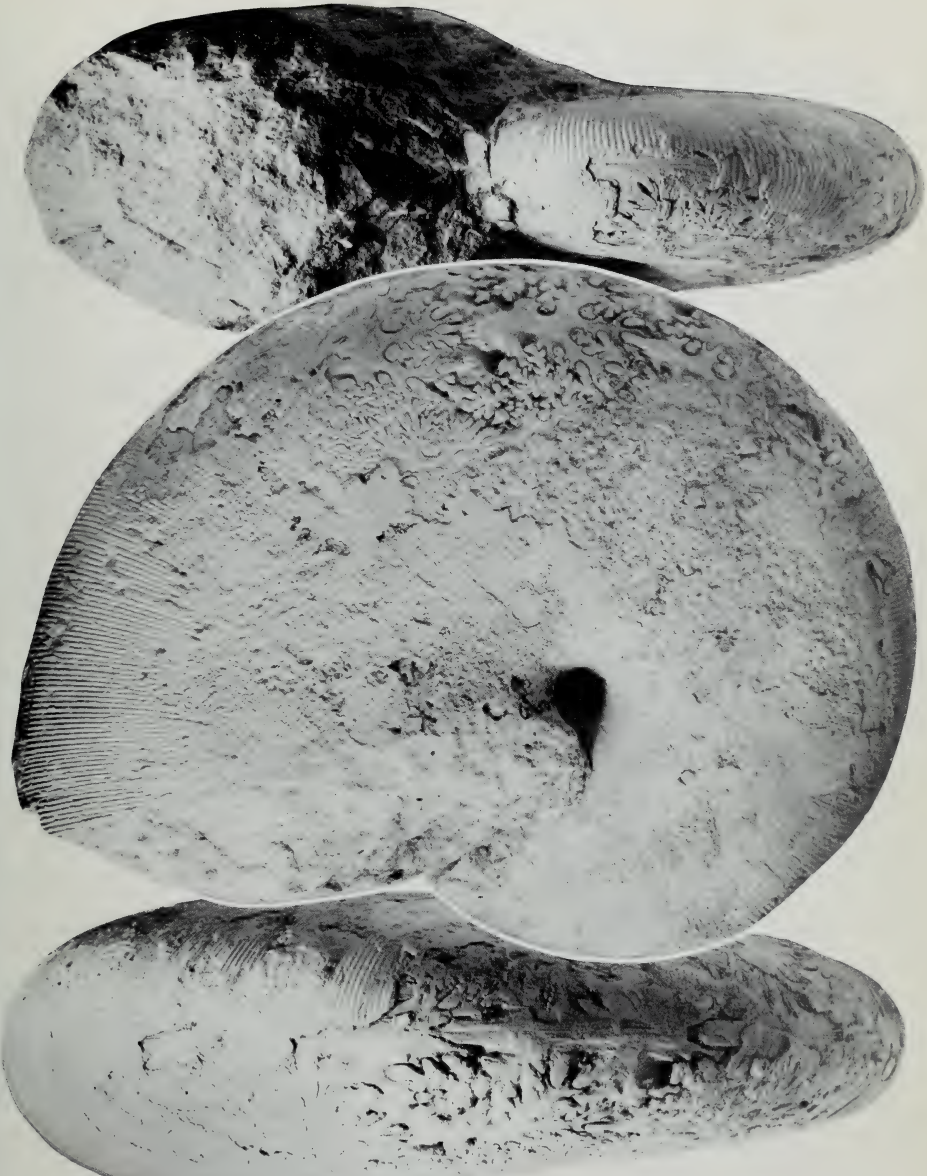


PLATE 10

Phylloceras (Hypophylloceras) velledae velledae (Michelin)
SAS Z1492a, Mzinene Formation, Albian V, Loc. 54, Mzinene River, Zululand. ×0·86 ; actual diameter 162 mm. (p. 360 ; see also Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 and Pls 8, 11.)

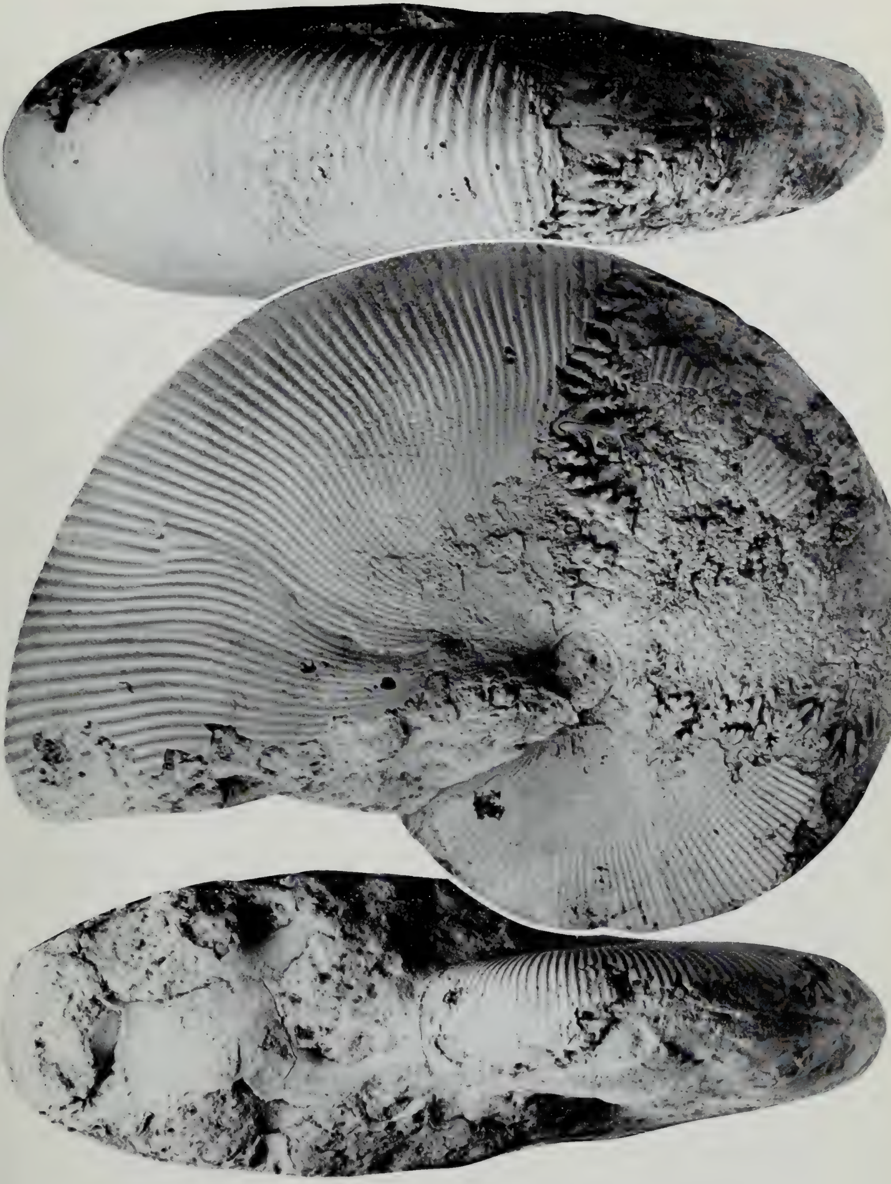


PLATE 11

Phylloceras (Hypophylloceras) velledae velledae (Michelin)
SAS Z1496, Mzinene Formation, Albian V, Mzinene River, Zululand.
× 0·85 ; actual diameter 169 mm. (p. 360 ; see also Pl. 4, fig. 5 ; Pl. 5, fig. 4 ; Pl. 6, fig. 1 ; Pl. 7, figs 2–3 and Pls 8, 10.)

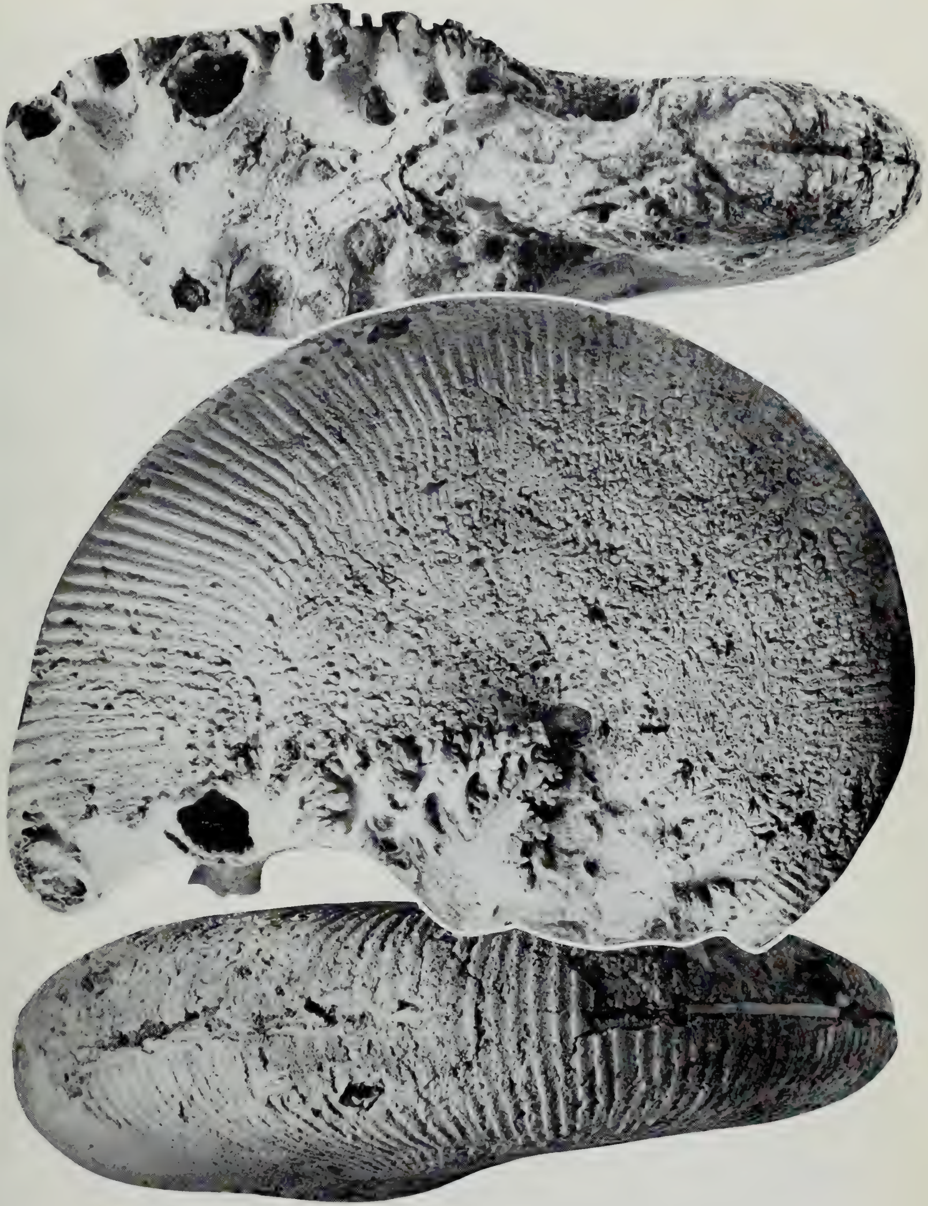


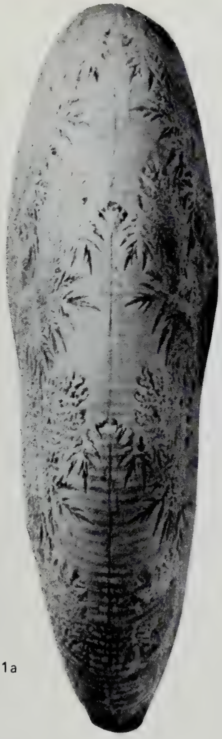
PLATE 12

Phylloceras (Hypophylloceras) mikobokense (Collignon)

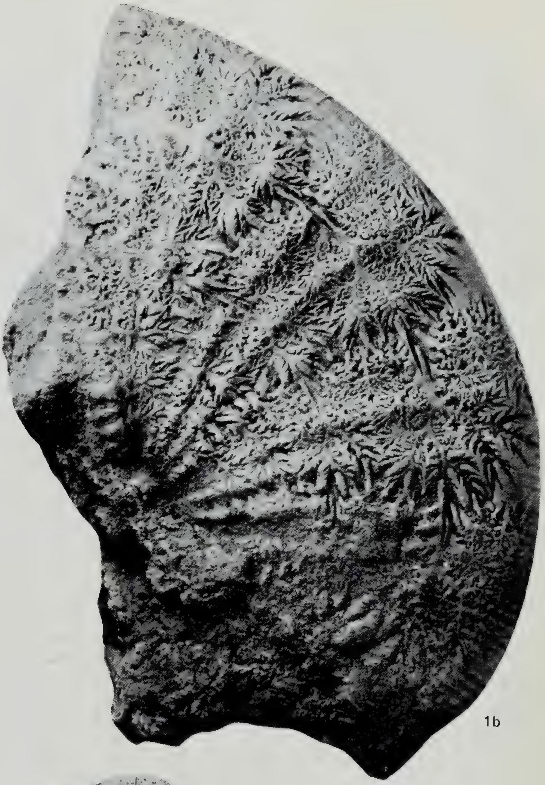
FIG. 1. SAS H163c/7, St Lucia Formation, Maastrichtian I, Loc. 20, Mfolozi River, Zululand. ×1. (p. 368.)

Phylloceras (Hypophylloceras) subalpinum ellipticum Kossmat

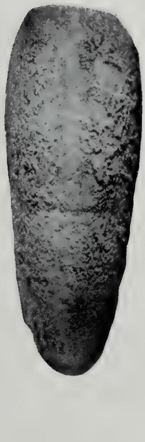
FIG. 2. BM(NH) C78666, Mzinene Formation, Cenomanian II or III, The Skoenberg, Mzinene River, Zululand. ×1. (p. 355 ; see also Pl. 4, figs 1–4 and Pl. 5, figs 2–3.)



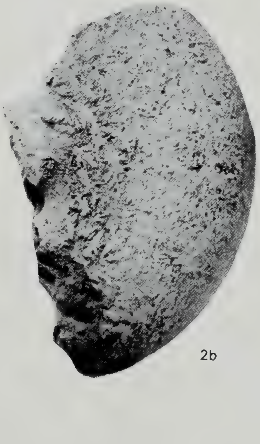
1a



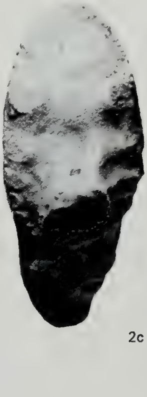
1b



2a



2b



2c

PLATE 13

Phylloceras (Hypophylloceras) velledae inflatum Collignon

FIG. 1. SAS Z1742, Mzinene Formation, Albian IV or V, Mzinene River, Zululand. × 1. (p. 362.)

Partschiceras umzambiense (van Hoepen)

FIG. 2. Holotype, TM 524, Umzamba Formation, Santonian or early Campanian, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). × 1. (p. 370.)

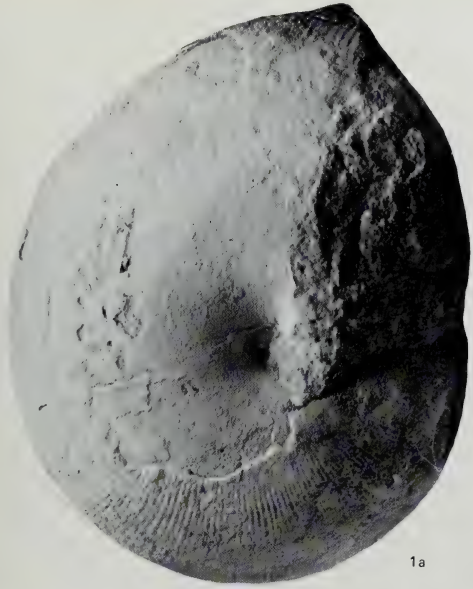
Phylloceras (Hypophylloceras) woodsi woodsi van Hoepen

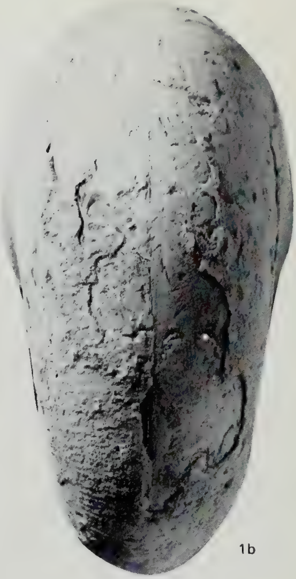
Umzamba Formation, Santonian or early Campanian, Loc. 1,
mouth of Umzamba River, southern Natal (Pondoland). (p. 366.)

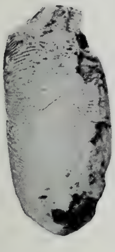
FIG. 3. Durban Museum specimen, mentioned by Spath (1921 : 50) as *Phylloceras nera* (Forbes). × 1.

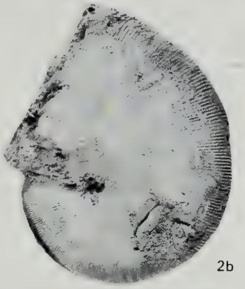
FIG. 4. Paratype, TM 534, × 2.

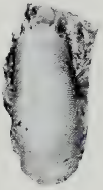
FIG. 5. Holotype, TM 537, × 2.


1a

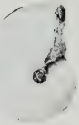

1b


2a

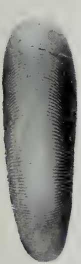

2b

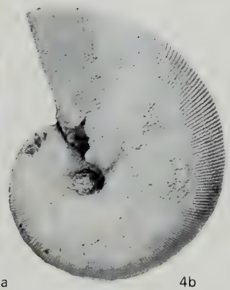

2c

3a

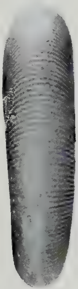

3b

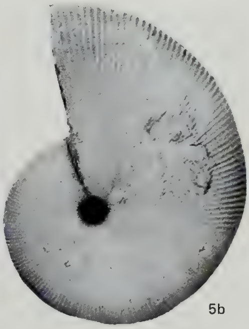
3c


4a


4b

4c


5a


5b

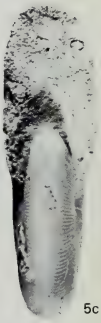
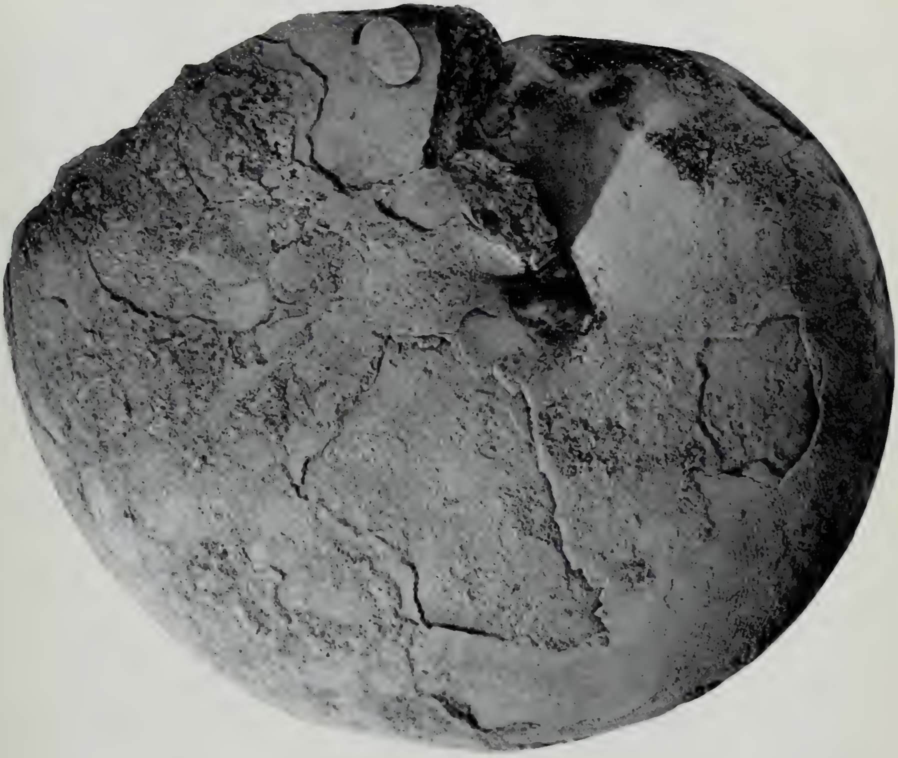

5c

PLATE 14

Carinophylloceras collignoni Klinger, Wiedmann & Kennedy
Paratype, BM(NH) C78640, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand. × 1. (p. 373 ; see also Pl. 15.)



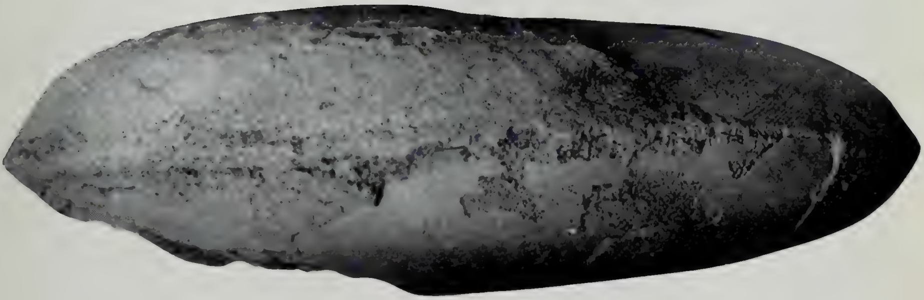


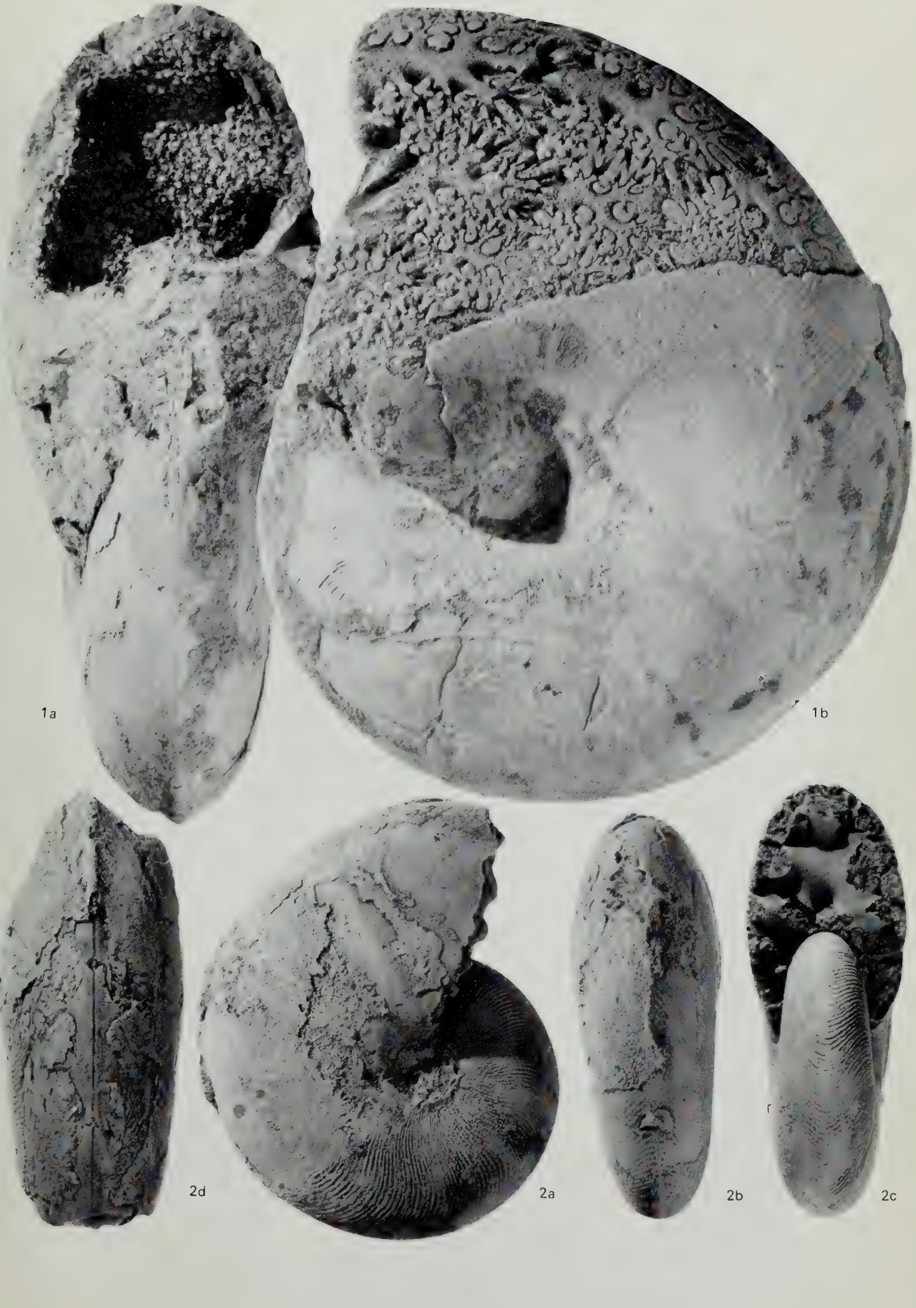
PLATE 15

Carinophylloceras collignoni Klinger, Wiedmann & Kennedy

Albian III, Mzinene River, Zululand. Both × 1. (p. 373 ; see also Pl. 14.)

Fig. 1. Paratype, BM(NH) C78644, Loc. 35 (Bed 2).

Fig. 2. Paratype, BM(NH) C78768, Loc. 36.


1a
1b
2d
2a
2b
2c

A LIST OF SUPPLEMENTS TO THE GEOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

---

1. Cox, L. R. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. Pp. 213; 30 Plates; 2 Text-figures. 1965. OUT OF PRINT.
2. El-Naggar, Z. R. Stratigraphy and Planktonic Foraminifera of the Upper Cretaceous—Lower Tertiary Succession in the Esna-Idfu Region, Nile Valley, Egypt, U.A.R. Pp. 291; 23 Plates; 18 Text-figures. 1966. £11.
3. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates; 64 Text-figures. 1966. £8.20.

3. Appendix. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.

4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates; 16 Text-figures. 1968. OUT OF PRINT.
5. Rhodes, F. H. T., Austin, R. L. & Druce, E. C. British Avonian (Carboniferous) Conodont faunas, and their value in local and continental correlation. Pp. 313; 31 Plates; 92 Text-figures. 1969. £13.10.
6. Childs, A. Upper Jurassic Rhynchonellid Brachiopods from Northwestern Europe. Pp. 119; 12 Plates; 40 Text-figures. 1969. £5.25.
7. Goody, P. C. The relationships of certain Upper Cretaceous Teleosts with special reference to the Myctophoids. Pp. 255; 102 Text-figures. 1969. £7.70.
8. Owen, H. G. Middle Albian Stratigraphy in the Anglo-Paris Basin. Pp. 164; 3 Plates; 52 Text-figures. 1971. £7.20.
9. Siddiqui, Q. A. Early Tertiary Ostracoda of the family Trachyleberididae from West Pakistan. Pp. 98; 42 Plates; 7 Text-figures. 1971. £9.60.
10. Forey, P. L. A revision of the elopiform fishes, fossil and Recent. Pp. 222; 92 Text-figures. 1973. £11.35.
11. Williams, A. Ordovician Brachiopoda from the Shelve District, Shropshire. Pp. 163; 28 Plates; 11 Text-figures; 110 Tables. 1974. £12.80.

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU